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THE GEOGRAPHY OF THE FLOWERING PLANTS

. *that grand subject, that almost keystone of the laws of creation,
Geographical Distribution.*”

CHARLES DARWIN
in a letter to Joseph Dalton Hooker in 1845.



THE GEOGRAPHY OF THE FLOWERING PLANTS

BY

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(Natural History)*

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AND
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PREFACE

THE manuscript of *The Geography of the Flowering Plants* was completed in the summer of 1939 and immediate publication was intended, but the vicissitudes of the war have caused its postponement until now.

In the seven years that have thus elapsed great changes have come about in the life of nearly every part of the world, and in two notable respects these changes are likely to increase interest in the study of plant geography. The spectre of starvation and the rigours of rationing have brought about a much more vivid appreciation of what man owes to the plant world; and the global military struggle has made familiar to the layman many of those more remote parts of the world (such as the islands of the Pacific Ocean) that are of special interest to the student of plant distribution.

On the other hand the war has brought chaos to the co-ordination of learning and research, and years are likely to pass before the advances in knowledge that may be expected from the opening up of hitherto little-known parts of the world can be fully recorded and integrated.

Therefore, although the text of this book has been as far as possible brought up to date, it must be regarded in the main as depicting the state of our knowledge at the outbreak of war, and subsequent advances must await full treatment at a later date.

This unavoidable delay in publication, though regrettable, has had one advantage. The plan of this book has permitted only a comparatively brief reference (notably in Chapters 3 and 14) to certain matters which are of considerable interest and about which the reader may well wish to know more, and it is now possible to refer to two other works in English which deal with them much more completely. These are the authorised translation of Wulff's *Historical Plant Geography* (292) and Cain's *Foundations of Plant Geography* (276). The latter, in particular, includes not only an up-to-date account of the evolutionary background to the subject (especially with regard to modern ideas on the origin of species), and of various questions relating to the distribution of plants in the past, but also a very extensive bibliography. Both books are valuable complements to *The Geography of the Flowering Plants*.

It is inevitable in a book of this kind that many facts are quoted without critical comment, since to verify them in detail would be impossible, but every care has been given to the selection of the sources from which they are taken. Also it must be remembered that there is no single complete modern revision of the whole group of the Angiosperms, nor, considering the amount of work it would involve, is there any such in prospect, and the literature is very scattered and often difficult to correlate.

As far as seems practicable the sources of all the major statements in the text are given in the selected bibliography at the end of the book, but there are four outstandingly comprehensive works to which I have had such constant recourse that they must receive special mention and acknowledgment here. They are *Index Kewensis* (131), *Das Pflanzenreich* (69), *Die natürlichen Pflanzenfamilien* (72, 73) and *Willis' A Dictionary of the Flowering Plants and Ferns* (263).

Further, with regard to examples and statistics, it should be borne in mind that these are useful chiefly for illustrative purposes. Figures must, generally speaking, be looked upon as relative, and of most value as a means of comparison. To treat them as absolute and immutable would be to misinterpret both the figures themselves and their function, for even when they are computations made specially for this book, they are ultimately based on what are, in many cases, no more than personal estimates and opinions. •

So many of my friends and colleagues have contributed, in one way or another, to the writing of this book that it is quite impossible to acknowledge in detail all the help I have received in this way, and I can only hope that they will one and all accept this general expression of my thanks.

I must, however, express my very special gratitude to my old master, teacher and friend, the late Sir Albert Seward, whose death in 1941 deprived the botanical world of one of its wisest and kindest figures. It was characteristic of him that he should find time to read the whole lengthy manuscript critically at a period which must have been most inconvenient for him, and it is a peculiar satisfaction to me to have this opportunity of paying a personal tribute to his memory. His many suggestions and comments, especially in connection with the geological history of the Flowering Plants, were of the greatest service.

My very grateful thanks are due also to my former colleague, Mr. J. E. Dandy, who has devoted a great deal of time to reading the proofs. His ready and generous help has been invaluable in many problems, and particularly in those touching the vexed question of plant nomenclature. Concerning this matter the use of the names at present regarded as correct has sometimes led to the supersession of particularly familiar names, and where this has happened the latter have been added in brackets. In the case of British plants the nomenclature follows that of the recently published "Check List of British Vascular Plants" (294), except that I have retained initial capital letters for certain of the species names.

The numbers in brackets refer to the entries in the Bibliography, which includes also a number of general works on plant geography not specifically referred to in the text.

For the excellent plant drawings I am indebted to Miss Lorna Pillow.

RONALD GOOD.

Hull, 1946.

ALLEN PAUL DRINKWATER

LIEUT., R.N.V.R.



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INTRODUCTION

The Importance of Plant Geography

(PLANT geography is that branch of botany that deals with the spatial relationships of plants both in the present and the past. Its aim is to record, and then if possible to explain, the distribution of plants over the world's surface.)

This book is arranged on a similar plan. The first part consists of a purely descriptive account of the facts of distribution in one great group of plants, and the second consists of a theoretical consideration of these facts and concludes with an attempt to give a generalised explanation of them.

Compared with many other aspects of botany, plant geography is remarkably free from technicalities and their attendant terminologies. It is naturally, too, an out-door subject rather than one involving exact experiment in a laboratory and its study needs neither complicated nor costly equipment. It therefore appeals not only to the trained botanist but also to many whose interest in plants, though just as real, is less academic, and especially those who delight in their gardens. For the same reasons it should be possible to prepare an account of the subject acceptable to all these, provided only that it incorporates, for the benefit of the less scientifically minded, an introduction to those aspects of biological thought and method of which some appreciation is necessary if the geography of plants is to be understood properly. Such an introduction is provided in these first pages, but they are in the nature of a preamble to the main parts of the book and the more scientific reader need not be detained by them.

Plant geography is so closely related, not only to many other branches of botany, but to zoology and anthropology, that it is a subject of great importance to man. The enormous advances that have been made in applied sciences make it ever more difficult to recognise in their proper proportions the foundations on which human civilisation rests and the influences that have determined the main trends of its development. Civilisation has been defined as man's gradual conquest of his environment, but how far this process has, in sober fact, gone is a matter for careful thought. In some ways certainly man's mastery over nature is complete enough. He has, for almost all practical purposes, annihilated space; he has explored and exploited the resources of the mineral world to a remarkable degree; he has gone far towards the control of infectious disease, especially in the warmer parts of the world.

These are great achievements, but they must not blind us to the fact that in other ways his efforts have been comparatively unavailing. His control of the elements, for example, can only be described as poor, and although he can often modify their dangers they not infrequently reveal their potentialities with disconcerting clarity.

Another direction in which he has been less successful, and which is of chief concern here, is his relation with the plant world, which still remains what it has always been, the only true basis of human economy. Naturally enough vegetation is as susceptible to man's destructive propensities as any other part of nature, and in many respects it can be as easily exploited by him, but unlike the rest he cannot entirely bend it to his will. Above all, there are two important things which,

with all his knowledge, he cannot do—he cannot appreciably control, under all conditions, the speed at which crops mature and ripen ; and he cannot grow every kind of plant where and when he likes. In consequence the business of maintaining and distributing his food supplies requires a complicated prevision and an intricacy of movement which makes it extremely vulnerable to disruptive factors. For the explanation of this the reader must refer to sources where the problems are dealt with at greater length (97, 216), but at this particular juncture in world history the statement itself needs no special demonstration. In the last six years the nations have presented one another with many and terribly imminent dangers, but behind them all has loomed the one ultimate and over-riding peril that the disorganisation of agriculture and transport arising from them will spread so widely and uncontrollably that there will come about, over much of the world, absolute dearth beyond remedy and the destruction by starvation of a great part of the human race.

Modern conditions have accentuated this danger and contemporary events have made its possibility all too clear, but it has always been in existence and the distribution of plants, which is one of the factual bases of it, has been a controlling influence in mankind's development throughout his history. It is no mere caprice that the earthly paradise depicted in the Book of Genesis—the Garden of Eden—is a place where, to use the words of the Authorised Version, there grew “every tree that is pleasant to the sight and good for food,” because that is simply the pictorial rendering of an age-long ideal.

But apart from myth there is abundant evidence of the way in which plant geography has determined the course of history and the destinies of man. To consider this evidence at length would be equivalent to writing a history of the human race and is therefore impossible here, but the more salient points must be stated.

The natural vegetation of any part of the world can, in general, be described as belonging to one or other of three types only (Plate 2). It is either forest of a sort, grassland of a sort, or some kind of desert. There are, of course, considerable areas where somewhat intermediate conditions prevail, but from the human point of view these are the three main conditions. In the forests the plants are mainly trees ; in the grasslands they are mainly grasses ; while deserts may be described as areas where the total plant life and cover are scanty and incomplete, producing neither woodland nor pasturage.

The potentialities of these three to a human population are obviously very different. Deserts are, by definition, unlikely to provide a sufficiency of food and such as there may be is likely to be of little value since it will not include the products of trees or grasses.

Forest, while it may in total contain large potential supplies, offers many obstacles to exploitation by man, unless he is at one or other extreme of his development. A very primitive human society, sparse in numbers, may derive sufficient from it, and modern industrial societies can remove and destroy it, but to most peoples this type of vegetation is a serious barrier to progress, because it deprives them of two prime necessities, space for expansion and the opportunity for an economic form of agriculture by which their supplies may be increased in proportion to their growing needs.

The grasslands, on the other hand, meet both these primary requirements, providing huge open spaces as stages for the playing of the human drama, and room wherein the most convenient and desirable forms of human food can be produced.

It is here, too, that the climatic conditions most suitable for the human race are to be found.

If the world distribution of these three types of vegetation is studied, it is seen that it follows fairly closely the distribution of certain climatic values. Briefly, deserts are found where the prevalent conditions are excessive heat or cold, usually accompanied by lack of moisture, at least at some seasons. Forests, conversely, are found where precipitation is high and especially where temperature also is considerable. The climate of some forest regions is not in itself unsuitable for man, but, as has been said, the nature of the vegetation militates against him. Grassland, however, generally reflects medium climatic values, where there is rain in sufficiency but not in excess and where the temperature is mild. In short it tends to have just the climate which is usually regarded as the best not only for the physical but also for the mental activities of mankind.

It may well be doubted whether primitive man consciously realised the climatic significance of the grasslands, but of their spatial advantages and of the ease with which animals could be hunted on them he must soon have become aware, and for this reason the association of man with this particular kind of vegetation is not hard to understand.

His dependence on the grasses for his own staple food, however, is an aspect of the subject which, by its very familiarity, excites much less interest than it deserves. To-day the pre-eminence of the grasses among the useful plants of the world is due to their double rôle of providing fodder from their vegetative parts and food from their fruits. The first of these two rôles is presumably the older, and with it the whole earlier history of mammalian evolution is intimately involved. The second is younger and its origin is mysterious. It is easy to imagine how, in the dawning of his intellectual powers, man might conceive the possibility of growing deliberately, in order to provide himself with food, plants whose fruits are large and conspicuous, but it is difficult to understand the circumstances by which his early agriculture became, as it did and as it has remained, concentrated upon the cultivation of grasses for the sake of their grain. For the most part the fruits of wild grasses are, in comparison with the fruits of many other plants, neither conspicuous nor bulky, and that their great potentialities as human food were so soon and so unerringly realised is one of the most intriguing sides of the story of primitive man, and may indeed be a valuable clue to problems which still remain to be solved.

But however it may have come about the development of mankind has been and presumably will long continue to be essentially a grassland development. Of the grazing or fodder aspect of this no more need be said here, but the subject of cereals as human food affords a peculiarly vivid picture of the influence of plant geography and a useful introduction to that study.

Although there are small but familiar exceptions it is true to say that even to-day, when diets have become so greatly diversified, the staple food of practically the whole human race is some kind of grain. Anything like a comprehensive list of the grains used would be lengthy, but of them all no more than half a dozen have an importance far greater than that of all the others put together. These are wheat, barley, rye, oats, rice and maize, the last named being on the whole less important than the rest. Broadly speaking, the first four are crops of temperate regions, the last two of tropical countries. That is to say, these are their present cultivation zones, but it is of more particular interest to enquire into their natural ranges. In detail this is a subject of great controversy, but in general it may be

said that wheat probably had its home somewhere in western or central Asia, barley and oats in rather more northerly parts of the same region, and rye somewhere more to the north again. Rice comes from the monsoon tropics of eastern Asia and maize, the only important New World grain, from somewhere in central America.

When maps showing the distribution of the earlier human civilisations are consulted it will be seen that these occur almost entirely in three parts of the world, namely western and central Eurasia, eastern Asia, and to a lesser extent in central America. That is to say, they have much the same natural distribution as the chief grain crops.

This correlation can be elaborated in many interesting ways and one or two may well be mentioned here.

Africa has conspicuously never been the site of a comprehensive and powerful civilisation. Whether or not it may have been the cradle of the human race, as some believe, it has remained the home of a loose-knit collection of comparatively primitive races. Nor has it any outstanding cereal of its own. Most of the African peoples have their own peculiar grains, but these are all of local significance and range, a point strikingly emphasised by the fact that the semi-industrialised African natives of to-day have adopted maize as their staple food and that its use is spreading to other parts of the population.

Temperate North America has contributed nothing of moment to the world's list of cereals and this is not unrelated to the fact that the native race of this part of the world was a scanty nomadic pastoral one, mainly without the localised and fixed type of agriculture which has always proved one of the foundations of human progress.

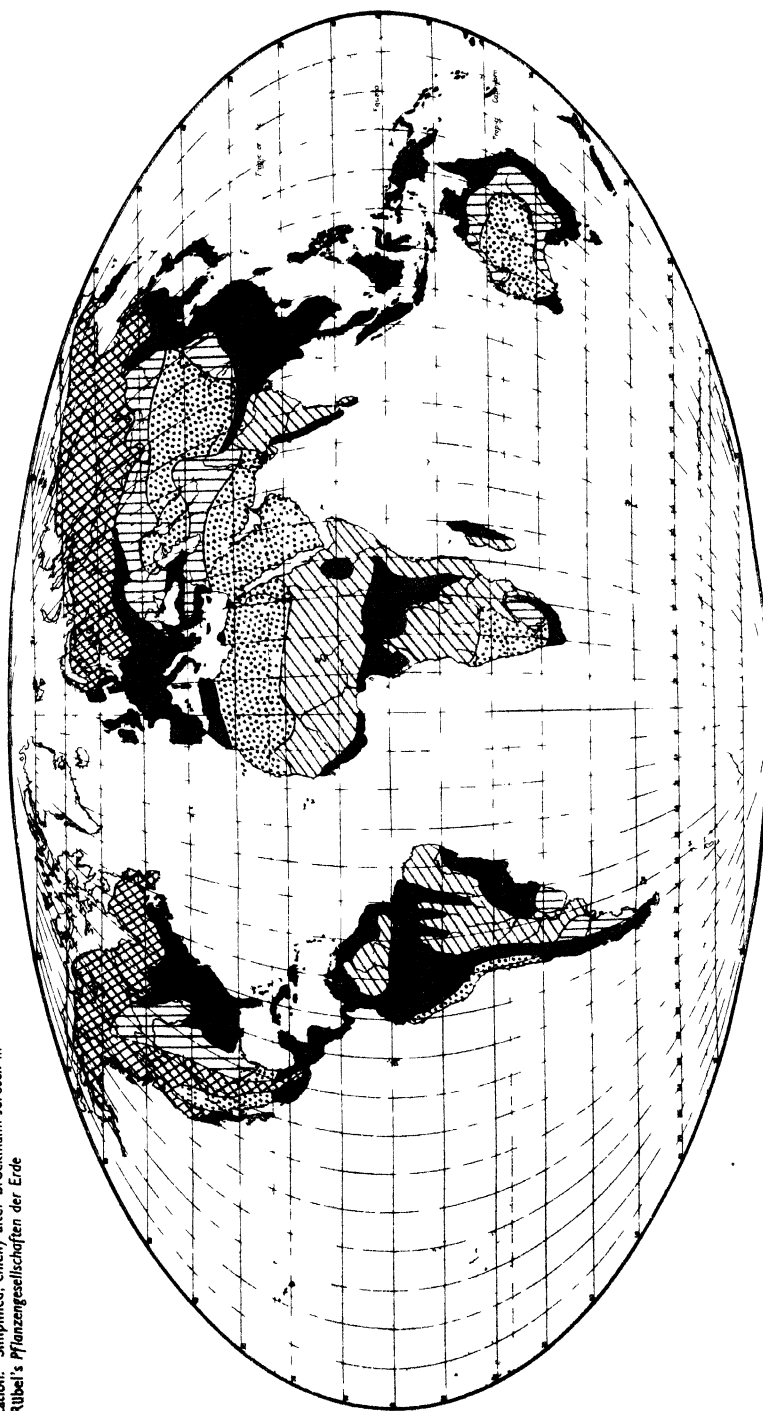
Until the period of European settlement the human population of Australia consisted of a sprinkling only of a race in the most primitive state of existence, comparable indeed to the Stone Age of Europe, and it is difficult to imagine that the absence of a well-characterised indigenous cereal is not a reflection of this low level of culture, or conversely, that the exploitation of some such crop plant would not have been accompanied by great changes in the mode and standards of life of the aborigines.

These instances show clearly enough, if only in one way, the relation between the distribution of plants and the development of man, but neither the one nor the other has grown up suddenly. Each is the outcome of a long and complicated series of events, extending in the case of the plants over many millions of years. Human history is much shorter and covers only the later chapters of the history of plants, but there is no doubt that where the two are concurrent a knowledge of each contributes greatly to an understanding of the other.

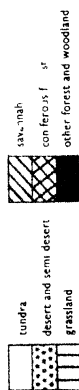
The plant geographer concerns himself not only with the distribution of plants in space but also with their distribution in time, and it is one of the purposes of this book to discuss some of the great changes in the distribution of plants that have taken place in the course of geological time. It will appear that the primary cause of these changes has been variation in the distribution of climatic values, but one of their most important aspects is that, acting through the intimate association already described, they have, during the short time that man has occupied the earth, been accompanied by equally great changes in the distribution of human populations. To this cause, for instance, are to be attributed at least two of the major features of human history—the repeated human migrations from the interior of Asia, which have occurred time after time almost throughout the historical

PLATE 2

Map of the World showing the distribution of Vegetation. Simplified, chiefly after Brockmann-Jerosch in Rübels Pflanzengesellschaften der Erde



Areas correct Distortion increasing towards border of map
Approximate Scale 1 000 000 000 (600 miles) along Equator
on Mollweides Homolographic Projection



period, and that gradual northward trend of the centre of world civilisation which is often called "the Northern March of Empire."

Thus it is to be seen in two quite different ways that plant geography is a subject so intimately connected with human affairs that however academic some aspects of it may seem, it is worth the careful attention of all whose aim and hope it is to reach some understanding of mankind and its difficulties. It can throw light not only on many present-day questions but also on many relating to the past. This being so, may it not also have some value as indicating the way in which some aspects of affairs at any rate may tend in time to come, and thus to do something towards lessening the greatest of all limitations under which man labours, his inability to see into the future?

✓Vegetation and Flora

Within the science of botany plant geography is most intimately connected with plant ecology, these together making up the wider subject of *geo-botany*, which comprehends all aspects of the relation between plants and the surface of the earth that is the substratum of their lives. Plant ecology is particularly concerned with the way in which plants are mutually related to one another and to the conditions of their habitat. Plant geography, on the other hand, is concerned primarily with the correlation between plants and the distribution of external conditions. The former is essentially physiological; the latter is essentially geographical. Expressed in another way, the difference is that between *vegetation* and *flora*, and a clear understanding of these two terms is important.

The chief features of vegetation reside in its quantitative structural characters because of their obvious influence on all other kinds of associated life. These structural characters are, as has been shown, closely related to climatic conditions, and hence the same kind of vegetation, that is to say the same kind of dominant growth form, tends to recur in many parts of the world. For example, deciduous woodland is found not only in the British Isles and other parts of Eurasia, but also in parts of North America, as well as elsewhere, and in all these places it possesses much the same general features and dimensions.

The word *flora* is a purely scientific term and therefore has no common usage (which is itself an interesting commentary on the conception behind the word *vegetation*), and its meaning is best expressed by extending the example employed in the last paragraph. Although the deciduous woodlands mentioned there are alike in their vegetational features they will be found on closer examination to differ greatly and perhaps entirely in their floral (or floristic) constitution. The vegetation will be the same in all cases, but the actual kinds of plants which comprise it—and which together compose its flora—will be different. The beech of English woodlands is not the kind of beech which grows in the North American forests, nor do either of these occur in the southern hemisphere, where their place is taken by other related species.

Just as vegetation is chiefly a matter of quantitative characters so flora is chiefly a matter of quality, in the sense that it concerns the family relationships of the plant life rather than its visual resemblances. The flora of a region is the total of the species within its boundaries, but the vegetation is the general effect produced by the growth of some or all of these in combination.

The Flowering Plants and their Classification

The plant kingdom as a whole can be divided into two parts or sub-kingdoms—the Phanerogams, comprising all the plants which reproduce by means of seeds, and the Cryptogams, comprising all those which reproduce by means of simpler structures called spores. None of the latter, which include ferns, mosses, seaweeds, fungi and the like, are concerned here.

The Phanerogams or Seed Plants themselves consist of two groups. In one the seeds are generally borne in cones and are not protected by any exterior structures except in so far as the cones themselves may shelter them. This is the group of the Gymnosperms (a word meaning “naked-seeds”), and it includes the Conifers and their allies. With these also we are not concerned.

In the other group, which is immeasurably the larger, the seeds are borne in flowers and are protected by being produced in enclosed structures called carpels. This is the group of the Flowering Plants or Angiosperms (a word meaning “concealed seeds”), and it is with these alone that this book deals.

The Flowering Plants or Angiosperms are the dominant plant group in the world to-day and represent the highest expression yet attained of plant evolution. They have gradually supplanted all other groups in prominence, and now comprise the great bulk of the vegetation of the land on all but some of the smallest areas. Practically all the plants used and cultivated by man belong to this group. They range in form from gigantic forest trees to tiny ephemeral herbs lasting but a few weeks. They have colonised practically all the land, they are common in fresh water and are even to be found occasionally in shallow seas. It is difficult to say how many different species of them there are, but there may well be upwards of 200,000.

For present purposes by far the most important general point about the Flowering Plants is that they represent the most modern type of plants and are the culmination, to date, of evolution in the plant kingdom. As might be expected from this they have a geological history much shorter than any of the other great groups of plants, and it is for this reason that this book deals with them alone. Time is a most important factor in matters of plant geography and it is therefore fundamentally unsound to treat together groups of plants whose length of history is widely dissimilar. To the older groups it is possible to apply generalisations which, owing to their shorter history, are quite inapplicable to Flowering Plants and conversely much of what is true of these plants cannot be applied to other groups because these are of far longer ancestry.

With regard to the definition which was given above it must be remembered that many of the Flowering Plants which are grown in gardens, and particularly some of the shrubs, have come from regions far away, and when cultivated in countries which are to them strange lands they do not always find the conditions which will enable them to bear flowers. Nevertheless these plants are true Flowering Plants, blossoming normally in their natural haunts, and the fact that they do not do so in gardens is no indication that they do not belong to this group. The only spore-bearing plants which are cultivated to any extent are some of the ferns, and their general characteristics are enough to distinguish them at sight from Angiosperms.

The primary classification of the Flowering Plants is into two great divisions, the Monocotyledons and the Dicotyledons, separated mainly by differences in the seeds. To the former, smaller, group belong such plants as grasses and lilies which, for the most part, have long narrow leaves with parallel veins ; while to the latter and larger group belong, in general, the plants with broad and net-veined leaves, including nearly all woody Angiosperms.

Each of these great divisions is classified into *orders*, based on very wide characters, chiefly of the flower. There are about a dozen orders of Monocotyledons and about forty of Dicotyledons. The order is too large a category to be of much practical importance and there will be no occasion to refer to it again.

Each order is classified into *families*. Some orders contain only a single family ; others have as many as twenty or thirty. The word *family* here has exactly the same meaning as the older term *natural order*, and this emphasises the special feature of the family, namely that it is, broadly speaking, the largest category in which a general superficial resemblance reveals the close relationship between all its members. All classifications to-day are, theoretically at any rate, natural, in as much as they are based on characters presumed to indicate evolutionary relationship as well as mere similarity, but obviously the larger the category the more diffuse and uncertain will be the inter-relationships within it, and the importance of the family is that it is, in effect, the largest reasonably natural unit for most practical purposes. In short, the contents of any one family may be regarded with some confidence as having had a fairly close community of origin and similarity of history.

Each family is made up of one or more *genera*, (the plural of the word *genus*), and just as in the *family* there are brought together plants of a general degree of relationship, so in the *genus* there are brought together the plants of a more particular degree of relationship. In practice this means that a genus usually comprises all the plants closely resembling one another. Thus, all the pansies and violets form one genus, and the lilies and willows respectively form others.

The *genus* may, above all others, be called the natural category. Families, despite their natural basis, are often so large and heterogeneous that there may well be some confusion between mere resemblance and real affinity, and many families are not entirely free from the suspicion of being to some extent unnatural for this reason. Genera, on the other hand, are smaller, and for that reason alone tend to be more natural ; but apart from this their characters usually emphasise this so much that for the most part they can be regarded reliably as true natural groups, that is to say as groups of plants the members of each of which have a common ancestry from a comparatively recent origin.

Finally, each genus consists of one or more *species*. In some ways the species is an unsatisfactory unit, for it is the subject of much controversy, and some reference to the cause of this must be made here. Difficulty arises primarily because the word has been current much longer than the idea of organic evolution, having been used originally to denote the different kinds of animals and plants which, according to the old cosmogony, had been *specially* created. In this sense the word had a normal conception and meaning, but unfortunately it continued in use after the doctrine of evolution became established and then came to mean (as far as can be expressed in words) any collection of individuals virtually like one another but more unlike any others and presumably the descendants of some one

earlier individual parent. This is a theoretical definition, and thus the species has come to have a subjective rather than an objective meaning.

It is this confusion that causes the practical problem. In the earlier view every species was an entity distinct from all others, with recognisable limits, and having the same kind of origin all were, in a sense, of equal value. In the later view the species is simply a collection of individuals related by descent, but how and to what extent it is usually impossible to say. Relationship can in fact only be estimated in terms of superficial resemblance, but the significance of similarity is a matter of personal opinion and hence it has come about that the word "species" scarcely means more at present than that it denotes a number of individuals which on account of their mutual resemblance are believed by fewer or more people to be descended from a single similar individual. This being so there is no real practical criterion of what constitutes a species and there are many different opinions. For this reason statements about species, and particularly estimates of their number, must always be treated with caution and regarded as indicative rather than absolute.

Families, genera and species are all important in plant geography. A family is not only a collection of genera but there is usually running through it some fairly well-marked structural feature (such as the capitulum of the Compositae) which is more or less peculiar to it. Because of this the distribution of families is often of considerable interest with regard to the possible place of origin of the main types of Angiosperm structure, and their significance in the evolutionary story. The larger families, too, are often particularly characteristic of certain parts of the world and this enables the salient features of different floras to be visualised in a way which is impossible with smaller categories.

The genus is the most natural category and can generally be accepted as combining together species which have had a common and close descent from a comparatively recent ancestor. This being a matter of great significance from the point of view of spatial relationships makes the genus the most important category for distributional studies.

The species is of value chiefly as a means towards statistical analysis. For such purposes, at any rate, species may be regarded as units of equivalent importance, and on this basis can be of great service in assessing geographical phenomena. For instance, to say that the flora of one region contains 100 species while that of another has 10,000, or to say that one genus has 5 species while another has 250, portrays the actual state of difference between the floras or genera in a particularly vivid way. Indeed, it is often only by using figures that qualitative resemblance or difference can be expressed quantitatively.

The Nomenclature of Plants

The nomenclature of plants, or the science of their names, is often a cause of bewilderment to those who are not familiar with its principles.

In the early days of botany, when the number of known plants was much smaller than it is to-day, there was no definite method of giving distinctive names to different kinds of plants and these could be distinguished verbally only by means of a short descriptive phrase embodying their more prominent characteristics. As the number of known plants increased this became more and more difficult

because longer and longer descriptions became necessary, and after a while great confusion arose.

The credit for removing the difficulty belongs to the great Swedish botanist Linnaeus, who flourished about the middle of the eighteenth century and whose method of naming plants is reckoned to date from 1753 (148). His solution was what is termed the binomial system, by which each kind of species of plant is given two names and two names only, the combination of names given to one species never being given to any other. There was really nothing startlingly original about this procedure because it is what in fact is done in the case of human beings in most countries, and Linnaeus' two names were indeed almost exactly comparable with the surname and Christian name of a person. His genius lay in applying this system to plant species and genera, and more particularly in doing so in such a way that no two different species possessed the same name.

The names were not, of course, called surnames and Christian names, but *generic* and *specific* names. Each distinct kind of plant was called a species and the various species were collected into genera according to their mutual degrees of resemblance. The specific name thus corresponds to the Christian name and the generic name to the surname. An example will be the best way of making the working of the system clear. All the species of buttercup were collected together into a genus to which the name *Ranunculus* was given, so that every kind of buttercup possessed the first or generic name of *Ranunculus*. Then each species was given a second and distinctive name, this being made as descriptive as possible and being reserved solely to the one species. The creeping buttercup, for instance, was called *Ranunculus repens* (the Latin for "creeping"), the hairy buttercup was called *Ranunculus hirsutus*, the bulbous buttercup *Ranunculus bulbosus*, and so on, and since each species had its own particular name confusion between them was avoided.

At first, and for a considerable period, this method proved almost perfect and in theory remains so to-day, but difficulties began to crop up when, after Linnaeus' death, others carried on his work. New species were constantly being discovered by all sorts of people, and it became the inevitable practice for the discoverer or describer of a new species to give it a name. There was no means of correlating this scattered work, and so it frequently happened that what was in fact one and the same species was given two or more different names by different workers ignorant of each other's actions. It then became necessary to decide which of the names was to stand and which were to be abandoned. In general the principle of priority was adopted by which the earliest or first given name was chosen, but priority was often difficult to establish and gradually a great deal of confusion grew up. It is enough here to say that it ultimately became necessary to compile a most complicated set of rules for the naming of plants, but even so there are still great difficulties. It not infrequently happens that to fulfil these rules familiar and long-established names have to be replaced by new and strange ones, and this, when the reason is not fully appreciated, causes much confusion and sometimes much heart-burning. The changes are, however, made in good faith with the intention of trying to make things easier ultimately.

Another feature of Linnaeus' system which tends to be misunderstood to-day was his use of the Latin language for the purpose. The reason is really an excellent one, namely, that Latin was then and indeed is even now the nearest approach to a *lingua franca*. Latin was in fact used as a substitute for a universal language

and in order to avoid the necessity of translating the names into various national tongues. It would probably have been impossible to invent any reasonable system of nomenclature without it, and it really needs no defence. Unfortunately, most of us are concerned only with our own language and in these circumstances the use of Latin seems pedantic. Quite apart from the fact that it is indeed not so, there is a stronger reason for using Latin names. The alternative to Latin names is to use national names; but national names have never been given on any system and have simply grown up by common usage and this varies from place to place. Thus a plant may be known by several English names in different parts of the country and what may be intelligible in one part may be meaningless in another. Furthermore, all the English names are likely to be meaningless, let us say to a German or Russian. The use of Latin names avoids this difficulty because a species has no more than one Latin name throughout the world.

It is one of the practices of nomenclature that specific names which are derived either from human proper names or from vernacular or generic names shall be spelt with a capital letter, and readers must therefore not be surprised to find some names with a capital and others without. The difference is not the expression of personal idiosyncrasy but is in accordance with usual procedure.

✓ The History of Plant Geography

✓ The history of the study of plant geography needs mention here only in so far as it throws light on the theoretical background of the subject and on its relations with other branches of knowledge. In brief it falls into five periods. The first, and considerably the longest, is the pre-Darwinian period, which lasted from the earliest times to the middle of the nineteenth century. This was particularly the ✓ period of exploration and discovery and its essential achievement was the gradual description of the world's plant life, that is to say the accumulation of the main facts of plant distribution. The next period, the Darwinian, was a short but most important one reflecting, as it did, the great revolution in thought which its name implies. Darwin and his scarcely less notable contemporaries, Wallace, Huxley and Hooker, early realised that the geography of living organisms, which in terms of special creation might be a matter for wonder but not for speculation, provided, in terms of evolution, one of its most valuable lines of evidence, and it is only necessary to read the *Origin of Species* (52) itself to realise the change that evolution brought to plant geography. Since evolution has ever since remained a fundamental tenet of biological thought plant geography is in one sense still in the Darwinian period, but it is more revealing to limit this stage to the years say from ✓ 1850 to 1875, which was the testing time of the new theory. The rest of the nineteenth century may be called the German period. During it a great many workers reinvestigated and reorganised the whole subject of the distribution of plants in the light of its new theoretical background and among them the German school of Grisebach, Drude, Engler and others was pre-eminent. With the turn of the century two new branches of botany—ecology and genetics—arose in spectacular fashion. The former in particular diverted to itself much of the interest formerly enjoyed by plant geography, and during this time, which may be called the period of ecology, floristic plant geography suffered a partial eclipse. Finally, the last twenty-odd years have seen not only the rehabilitation of plant geography, mainly as a result of stimulating new theories relating to it, but what is even more

CORRIGENDA

- p. 95 Fig. 22 The Cape York Peninsula (north-eastern Australia) should be black.
- p. 99 line 40 Delete " the Canaries."
- p. 100 line 43 For " New Guinea " read " north-eastern Australia."
- p. 104 Fig. 31 For " *arborea* " read " *tomentosa*."
- p. 104 Fig. 32 Irmscher's map is in error in showing a ring round the Azores instead of round Madeira.
- p. 105 line 26 For " Bolivia, Chile " read " South America."
- p. 112 Fig. 42 For " *Astelia montana* " read " *Collospermum montanum*."
- p. 113 Fig. 43 For " sections " read " subgenera." The outline of B should be extended to include New Guinea.
- p. 113 lines 5-8 Read " one in the Marquesas, one in Tahiti, one in New Caledonia, one in New Guinea, two in Australia and Tasmania, nine in the New Zealand region, one in Reunion and one in South America."
- p. 171 line 18 For " 16 species, all " read " 22 species, mostly."
- p. 188 line 22 For " (274) " read " (279)."
- p. 193 Fig. 50 After " about " insert " half."
- p. 194 Fig. 51 For " about natural size " read " somewhat reduced."

important, much progress towards a proper synthesis of it with ecology, genetics and other aspects of botany which, far from being its rivals, are in fact its close allies. To-day, the study of plant geography has recovered much of the position it held seventy or eighty years ago. There is once more evidence that it may hold the key to much that is hidden and that it must therefore receive the proper measure of attention which it merits not only on this account but also because of its intrinsic interest.

PART ONE

CHAPTER 1

THE GEOGRAPHY OF THE WORLD

IN plant geography almost all aspects of the physical geography of the world are involved, but there are four subjects in particular of which an adequate understanding is so essential that a brief account of them is desirable here. They are the continents and oceans, the islands, the mountains, and the deserts.

✓ Continents and Oceans

The continental land masses of the world are in effect six in number, namely, Eurasia, Africa, Australia, North America, South America and Antarctica. The last named has now virtually no plant life and is covered with ice and snow, although it possessed a considerable vegetation in former ages.

The distribution of these masses in respect of the equator is such that the northern and southern hemispheres are almost exactly the opposite of one another, so that where there is land in the north, there is sea in the south, and *vice versa*. The Arctic Ocean in the north is balanced by the antarctic continent in the south, and so on. Arising from this, the distribution of the world's land masses can be described concisely in two useful ways. It may be pictured or represented by two cogwheels, each with three teeth, fitting into one another, the one wheel being the land of the northern hemisphere and the other the oceans of the southern hemisphere. A model made on these lines, with the land wheel black and the sea wheel white, is quite a good rough diagrammatic representation of the map of the world.

It will be apparent from this that the northern hemisphere is predominantly a land hemisphere and the southern one of sea, and in fact the general distribution of land can also be described as having the form of a more or less continuous northern ring from which three branches extend southward across the equator to varying distances.

This peculiar distribution of land leads to what is probably the most significant of all geographical features from the point of view of the general geography of plants and that which does more to explain the facts to be presented below than any other. It is that while in the higher northern latitudes there is a continuous belt of land all round the world, this belt becomes more and more incomplete towards the south, until in southern temperate latitudes there is practically no land at all.

The three extensions southward from this northern belt are South America, Africa, and Australasia with Malaya, and they differ considerably. The first reaches further south than the others and tapers to a point; the second is blunt and does not extend far beyond the Tropic of Capricorn; the third is intermediate in length and, beginning as an archipelago, ends in a detached continent.

But there is a further point about the continents which is apparent only if the distribution of the contours of the seas is studied. If a bathymetric map of the world (Plate 3) is examined, it will be seen that along some parts of the edges of the continents the passage to great depth is very rapid so that deep water lies close to the actual outlines of the land, but that in other parts the seas, for a considerable distance out from the coast, are shallow, the sudden deepening being much further away. Always, however, there is some point at which the waters become suddenly much deeper. The full significance of this will be discussed at greater length in Chapter 20, but it will be clear enough here that this sudden deepening of the sea marks the real edge of the continents and that where this is far seaward of the actual coast line this is because the edges of the continents lie at such a level as to be shallowly submerged. In other words, the absolute level of the edges of continents varies considerably. In most places they stand clear of the water to their very boundaries, but in others they pass gently below the sea level before their actual abrupt edges are reached.

This being so, the seas of the world can be classified into deep seas or oceans proper, bounded by the true edges of the continents, and shallow or marginal seas which are really shallow flooding of the peripheral parts of continents. These latter are appropriately called epicontinental seas. As has been said, this distinction and its meaning will be referred to again later, but it is of immediate importance here in connection with the classification of the islands of the world, which must next be described.

Islands

The number of islands in the world is very great, but the absolute figure is of no particular concern here, their size and distribution being of much greater importance. Obviously all land masses are in one sense islands since there is none which completely girdles the earth, but convention restricts the use of the term island to areas which are conspicuously less than those which habitually go by the name of continents. Greenland is generally described as the largest island and is considerably smaller than Australia or Europe, the least of the continents. Other large islands are Baffinland, Japan (three islands), Sumatra, Borneo, New Guinea and Madagascar, while on a somewhat lesser scale, Great Britain, Celebes and New Zealand (two islands) may be added.

Islands of what may be called second size are very numerous and include several in the Arctic, Iceland, Ireland, Newfoundland, Sardinia, Sicily, Ceylon, Formosa, Sakhalin, Vancouver, Cuba, Hayti, Java, Timor, Luzon and Mindanao (Philippines) and Tasmania. Smaller again are Jamaica, Porto Rico, Trinidad, Crete, Cyprus, Corsica, New Caledonia, and a number of the islands in the Malayan Archipelago.

Lastly, there are certain groups of smaller islands and a number of very small isolated islands. These are too numerous to be mentioned in full, but this is a good opportunity for listing those of special botanical interest and of giving a rough indication of their whereabouts. It is easiest to do this ocean by ocean.

In the Arctic Ocean are Jan Mayen, half-way between Norway and Greenland, and Bear Island, half-way between Norway and Spitzbergen.

In the North (extra-tropical) Atlantic are, first, the three groups off Portugal and North Africa, namely Madeira, the Canaries and, furthest from land, the Azores. On the west side of this ocean are the Bermudas and most of the Bahamas.

In the Tropical Atlantic are, first, the smaller islands of the West Indies ; second, the Cape Verde Islands, off Senegal ; third, the group of Fernando Po and St. Thomas, close to the coast in the Gulf of Guinea ; and fourth, St. Helena and Ascension.

In the Indian Ocean the Comoros, the Aldabra Islands, the Seychelles and the Mascarenes (Mauritius, Réunion and Rodriguez) lie respectively north-west, north, north-east and east of Madagascar ; Zanzibar is close to the African mainland a little south of the equator, and Socotra lies off the tip of Somaliland.

Off the south-west coasts of India are the Maldives and the Laccadives, while in between Burma and Sumatra come the Andamans and Nicobars. The islands just west of the latter are not important, but considerably further south are two very small and isolated ones, the Cocos Islands and Christmas Island.

In the North (extra-tropical) Pacific there are three remarkable festoons of islands between China and Alaska, namely the Liu Kiu (or Riukiu) Islands between Formosa and Japan ; the Kuriles between Japan and Kamchatka ; and the Aleutians between Kamchatka and Alaska.

Further south, in the tropics, the islands are innumerable, since they comprise not only many in the Malayan Archipelago, but also almost all the Pacific Islands. Many, especially of the latter, are merely coral atolls and of little botanical interest, but the following groups are all of some, and mostly of great, importance. It is convenient to list them from west to east.

Leaving aside the various very small islands of the Malayan Archipelago there comes first the Bonin and Marianne Islands, south of Japan, and the Caroline and Marshall Islands, east of the Philippines. South of these, and forming a wide curve east and south-east of New Guinea, are the Solomon Islands and the New Hebrides. A little east of the latter are the Fiji Islands and the groups of Samoa and Tonga. To the north-west of these are the Gilbert and Ellice Islands, while further to the east are the Society Islands, the Tuamotu Islands and the Marquesas. Far north of these last, almost on the Tropic of Cancer and about midway between Asia and America, is the very important group of the Hawaiian Islands of which the largest is of considerable size. Finally, far removed from any of the above and not far to the west of Ecuador, lie the Galapagos Islands.

In the South Pacific there are very few islands, but each of them is of special interest. North-west of New Zealand are the Lord Howe Islands and Norfolk Island, while north-east and east respectively of New Zealand are the Kermadecs and the Chatham Islands. Far to the east of these, about midway between New Zealand and America, is Pitcairn Island, and about half-way between it and America is Easter Island, famous for its strange statues. Lastly, not far from the Chilean coast, is the small group of which Juan Fernandez is the chief island.

There remain to be mentioned a number of tiny and very scattered islands situated in the great continuous sea surrounding the antarctic continent and which it is convenient to call the South Temperate Oceanic Islands. The flora of these islands is in total small but of peculiar interest, as will be seen later, and it is appropriate here to give a list of them. They are, working east from the tip of South America, the Falkland Islands, South Georgia, the Tristan da Cunha group and Gough Island, Marion Island, the Crozets, the Kerguelen Archipelago, Heard Island, St Paul and Amsterdam Islands, and Macquarie Island.

On the basis of their positions with regard to the continents, two sorts of islands

are generally distinguished. Some, including most of the larger islands, arise from the submerged shelves of the continents and are therefore called continental islands. Others, including the great majority of the smaller islands, rise directly from the floors of the deeper oceans and are therefore termed oceanic islands. The British Isles, Japan, and the members of the Malayan Archipelago are good instances of the first type and the various Pacific islands are good examples of the second.

Biologically this distinction, though somewhat arbitrary, is a very important one, because the criterion employed is really that of isolation. Continental islands, as integral parts of a continental mass, obviously have a close connection with the adjacent mainland and this is reflected in their plant and animal life. Oceanic islands, on the other hand, have no such connection although they may be situated fairly close to continents. They are quite independent of any large land mass and thus their biology presents features and problems of the greatest interest. In their case their isolation has been the predominant factor in controlling and determining their floras and faunas.

For this reason oceanic islands, and especially the more isolated of them, are of particular interest to the student of plant geography (117, 129, 251), and a good deal will be said about them later. In view of this it is not inappropriate to tabulate here, together with their distances from the nearest mainland or large islands, those to which most frequent reference will be made later. They are:

The Hawaiian Islands .	3,000	miles from Japan ;	2,000	miles from America
Kerguelen . . .	2,500	„ „	Australia ;	2,100 miles from Madagascar
Tristan da Cunha .	2,200	„ „	America ;	1,800 miles from Africa
Tahiti . . .	2,200	„ „	New Zealand	
Samoa . . .	1,700	„ „	„ „	
Fiji . . .	1,300	„ „	„ „	
St. Helena . . .	1,200	„ „	Africa	
Ascension . . .	900	„ „	„	
New Caledonia . .	800	„ „	Australia	
Rodriguez . . .	800	„ „	Madagascar	
The Azores . . .	800	„ „	Portugal	
The Galapagos Islands	700	„ „	America	
The Bermudas . . .	650	„ „	„	
The Seychelles . . .	650	„ „	Africa and Madagascar	
The Kermadecs . . .	600	„ „	New Zealand	
Mauritius . . .	500	„ „	Madagascar	
Norfolk Island . .	450	„ „	New Zealand	
Réunion . . .	400	„ „	Madagascar	
Juan Fernandez . .	400	„ „	Chile	
Madeira . . .	350	„ „	Africa	
Lord Howe Islands .	350	„ „	Australia	
The Comoros . . .			Between Madagascar and Africa	

The position of the above islands and of certain others is shown in Plate 3.

~~M~~ountains

The importance of mountains in plant geography lies in the fact that as altitude increases the climate tends to become more and more temperate or frigid in character, so that a mountain at a lower latitude has, in its higher parts, a climate very like that prevailing at sea level at higher latitudes. Owing to this a mountain nearer the equator is often able to support species, if not a whole vegetation, characteristic of or even identical with species or vegetation occurring at sea level further north. Moreover, since high altitudes are generally combined into mountain ranges which may be of great length, the mountain systems of the world often provide connecting links or paths of spread for plants.

In the broadest sense the great mountain systems of the world are only three in number, namely the western American system comprising the Rocky Mountains in North America and the Andes in South ; the Euro-Asian-Australasian system of the Old World, comprising the Pyrenees, Alps and Caucasus, the Sino-Himalayan mountains, the Central Asian plateaux, the mountains of Malaya and those of eastern Australia ; and the very different (both in size and form) African system.

But the picture is too complicated to be painted in quite such bald terms, however desirable it may be to simplify matters, and a more detailed classification must be made if all the necessary facts are to be revealed. On this basis the mountains are best described and arranged as follows.

The great western American mountain chain consists of two systems with distinct names, the Rockies in the north and the Andes in the south, but these are really only parts of one great whole which reaches, in a more or less southerly direction, from Alaska in the north to Cape Horn in the south, that is through the whole length of the continent of America. It is not unnaturally least obtrusive in the narrow isthmus of middle America, but even here it reaches elevations of over 12,000 ft. In the Rockies the greatest heights are in the extreme north-west (Mts. McKinley, Logan and St. Elias approaching or exceeding 20,000 ft.) and in Mexico (Popocatepetl, *c.* 18,000 ft.). In the Andes the highest mountain is Illampu, *c.* 25,000 ft., in latitude 16° S., but almost equally high peaks are scattered further north and south.

In eastern North America is the minor north-south range of the Appalachians, and in South America the south-eastern part of Brazil is also mountainous. It must also be remembered that Greenland is almost entirely an elevated plateau, but owing to the high latitude this is not very significant biologically.

In Europe the chief ranges are the Pyrenees, up to 11,000 ft. ; the Alps, up to 16,000 ft. ; the Apennines, up to 9,000 ft. ; the Carpathians, up to 9,000 ft. ; the Caucasus, up to 19,000 ft. All these ranges are more or less west to east, as are also the Atlas Mountains, which although in Africa belong to the same general system and which attain a height of nearly 14,000 ft. In addition to these the Balkans are almost entirely mountainous. In the north of Europe also there are two elevated regions, western Norway, where there is a height of 8,500 ft., and the Urals, where the highest point is some 5,000 ft. Both these latter systems run north and south.

In Asia the mountain systems are so vast and so complicated that without going into excessive detail it is possible only to describe them very generally. First, from the Bosphorus to north-west India there stretch a series of ranges mostly of medium height but containing a few great peaks such as Ararat, *c.* 17,000 ft.,

all running approximately west and east. Next, south-east of this area, much of the Indian Peninsula is mountainous, culminating in Adam's Peak and other heights of about 8,000 ft. in Ceylon. The main ridge of this system is along the west coast of India.

Lastly, the whole of the vast triangle N.W. India-Kamchatka-Siam is one huge and complex system of multitudinous mountain ranges comprising the most extensive area of elevated land in the world as well as all the highest altitudes. For most of the south side of this triangle runs the huge wall of the Himalayas themselves, a whole plexus of ranges culminating in the extreme world height of Mt. Everest, 29,000 ft. Northwards the Himalayas pass into the highly elevated Tibetan plateaux and these again north into the plateaux and ranges of North China and eastern Siberia. The axes of all these ranges are approximately west to east, but in Manchuria, Korea, Japan and Kamchatka they become more or less north and south following the coast line.

Passing back to the south-east of Asia, we are confronted with one of the major features of world relief. At the junction of Burma, Tibet and China the great west-east mountain chain which we have traced all the way from the Pyrenees to and through the Himalayas suddenly changes its course and the constituent ranges turn southwards, continuing north and south through Burma, Siam and Annam. Many of the mountains are of great elevations, but this region as a whole is not very well known and it is best to avoid figures which may be misleading.

The main line of this system is along its centre and runs right down the Malay Peninsula and passes into the Malayan Archipelago. The geography of this latter region is broken and scattered, but it can be said that the main mountain axis of the Malay Peninsula is continued in its main form in a curve through Sumatra and Java and the Lesser Sunda Islands. In both the former islands heights of over 12,000 ft. are recorded. Practically all the other great islands of the Malayan Archipelago are mountainous, although the axes of their ranges do not follow any well-defined line. In Borneo, for instance, Mt. Kinabalu is over 12,000 ft., and there are peaks of over 10,000 ft. in the Philippines. Further east again, in New Guinea, the general west-east trend of the mountains is once more apparent, and here also there are similar heights. In Australia the main mountain system is that which follows the east coast down into Tasmania, thus running north and south, and this may be regarded as the ultimate stretch of the great mountain line which begins in western Europe. The highest point here is Mt. Kosciusko, *c.* 7,000 ft., in New South Wales. Finally, New Zealand exhibits strong relief, culminating in Mt. Cook in South Island, which exceeds 12,000 ft.

In Africa the mountain system is rather different from elsewhere in the world. A ridge of elevated land runs north and south all the way from the Red Sea to the Cape. In the north there is the plateau of Abyssinia, with peaks exceeding 15,000 ft., and in the extreme south-east the mountains of Natal and the Cape Province form a more or less definite range attaining, locally, heights over 10,000 ft. Between these two areas the highest land consists largely of a number of very distinct and isolated mountains surrounding Lake Victoria. Nothing quite like these mountains exists elsewhere and they are frequently referred to as "island mountains." Chief amongst them are Kilimanjaro, nearly 20,000 ft., Mt. Kenya and Ruwenzori, nearly 17,000 ft., and Mt. Elgon, nearly 15,000 ft.

In addition to these there is a secondary series of mountains close to and parallel with the west coast south of the Gulf of Guinea.

Finally, a series of separate mountain massifs form a line between Abyssinia and the Atlas Mountains, thus forming as it were a series of stepping stones across the Sahara, and they are for this reason noteworthy. They are comparatively little known, but it is certain that some at least of them reach heights of 12,000 ft. It may be added that Madagascar is also mainly mountainous.

Deserts

Everyone knows what is meant in general terms by the word desert, but it is difficult to define it scientifically. Heat and drought are the commonest characteristics of deserts, but the two are not always combined, and deserts may, in fact, be either hot or cold, according to their latitude and altitude. In all, however, there is, for one reason or another, a deficiency of available moisture, and this is usually due to lack of rain. Botanically deserts have been defined as areas where, because of the climatic conditions, there is less than a continuous covering of vegetation, and this criterion includes also the entire absence of it. It is not easy, however, to know exactly where the line is to be drawn, and this definition breaks down if applied too narrowly.

Actually, although these points merit mention, there is no need here to attempt a rigid definition, and it will suffice to give a short survey of those parts of the world to which the name desert is generally applied. It may, however, be noted that they are, roughly speaking, those areas where the annual rainfall measures less than 10 ins. (Plate 23).

Deserts are for the most part to be found on the leeward side of mountain ranges because the heights discharge the rain-bearing clouds from the sea before they pass further inland. This is specially true of the warm deserts, which may be mentioned first.

The North American warm desert exemplifies this well, lying as it does between the constituent ranges of the southern Rockies. A similar intermontane desert occupies part of northern Mexico. Both these have elevations of several thousand feet.

In South America the arid parts of western Argentina are similar, but there is also the coastal and more tropical desert of Peru and Chile.

The deserts of Africa and Asia must, in part at least, be considered together because the greatest desert in the world covers parts of both continents. This is the great series of varying dry regions which stretches, with but few breaks, all the way from the west coast of North Africa to north-eastern Mongolia, and which has six main constituent areas. Of these the Saharan, Arabian and Persian deserts are warm deserts, while those of Turkestan, Tibet and Mongolia (Gobi) are mostly cold deserts.

The Sahara is, in a popular sense, the most typical and absolute of all deserts, and over much of it the surface is mobile sand and bears no plant life. This is, however, by no means continuous but is broken by mountains and oases. The Saharan, Arabian and Persian deserts form a more or less single belt of dry lands all the way from north-west Africa to north-west India. It is also noteworthy that this great region is less intimately associated with mountain ranges than most deserts.

Much of the western part of southern Africa is also arid, and this area comprises the well-known Kalahari and Karroo deserts. These lie amongst or inland of the mountainous parts of Cape Province.

Finally, there is the great central warm desert of the interior of Australia, which covers much of Western Australia and South Australia and the southern part of the Northern Territory. It illustrates well another feature often seen in deserts, namely, that they occupy the regions most distant from the coasts. The moisture-laden winds from the sea tend gradually to lose their water as they pass inland and distance has much the same result as that of a single mountain range.

The three chief cold deserts of the world have already been mentioned incidentally since they are part of the vast African-Asiatic desert. Among them, the Turkestan desert is the least extreme and has a fairly well-developed vegetation.

Both the Tibetan and Gobi deserts are good examples of cold deserts in which the low temperature is due to great elevation. Both, too, consist chiefly of the plateaux between mountains. The Tibetan plateau desert is often called "the roof of the world" and has an average elevation of some 15,000 feet. The Gobi desert in general exceeds 5,000 ft. The most important climatic feature of these deserts is the variation of temperature during the year, for a greater part of which they are exceedingly cold. Incidentally, even in warm deserts there is generally a great difference between day and night temperature.

In conclusion Antarctica is in one sense at any rate a cold desert because it is permanently ice-bound, and for this reason affords no habitats for flowering plants. There is no actual lack of moisture, but it is frozen into an unavailable form. Some parts of the Arctic are the same.

To summarise, the desert regions of the world comprise the warm deserts of North America, Mexico, South America, the Sahara, Arabia, Persia, southern Africa and Australia; the cold deserts of Turkestan, Tibet and Mongolia; and the ice-bound land surfaces of the polar regions.

Map Projections

It is almost impossible to depict exactly, on a flat surface like a page of paper, the surface of a sphere, and maps of the world as a whole or of any large part of it therefore almost inevitably contain some distortion unless very complicated and impracticable outlines are used. Various methods, often involving rather abstruse mathematics, are employed in order to reduce this distortion and one or two of these methods, or projections as they are called, require comment here.

The simplest method is perhaps that of picturing the world as it would appear if seen from a very long distance away, but since this view would reveal only the half of the sphere nearer the observer, the whole globe can only be shown thus by two separate circular maps. For most purposes this is a great drawback, but occasionally, as, for instance, when the polar regions are to be mapped, such a polar stereographic projection has its uses, and it is employed in one or two cases in this book.

The commonest of all projections is Mercator's projection, which shows the surface of the world in rectangular form, but this is only achieved at the expense of a seriously increasing distortion away from the equator. For everyday political maps whose interest centres in lower latitudes this disadvantage can be neglected, and this explains the constant use of this projection in simple generalised

maps, but for scientific purposes it is almost useless since it distorts not only the relative position but also the relative size of land masses. Moreover, even this distortion is not constant but increases towards the poles. For these reasons Mercator's projection is particularly unsuitable for problems of plant geography and no use at all is made of it here.

For all but very special purposes Mollweide's projection, in one or other of its forms, is perhaps the most convenient since it removes many of the drawbacks of Mercator while still permitting a fairly simple total outline. Mollweide's projection shows the world as an ellipse having the equator as its longer axis. It is an equal area projection, so that the relative sizes of different parts of the world are true, and this is a point of great value. On the other hand, there is some distortion of shape, especially towards the ends of the ellipse, but if, as is usual, Africa is made the central feature, this disadvantage is much reduced.

Although far from perfect it is difficult to find a better projection than that of Mollweide if the shape of the map is to remain continuous and simple, and since this is essential when biological problems are under discussion his projection is used almost exclusively in this book.

It need only be pointed out further that, with regard to maps showing less than the whole world, the smaller the area depicted the less important are problems of projections until, where quite small areas are concerned, the lines of latitude and longitude can be drawn truly horizontal and vertical without appreciable distortion.

Definitions

Most parts of the world have received their names without particular regard to biological problems, and hence, when these questions are at issue, it is sometimes necessary to refer to areas which have no convenient comprehensive names.

It is, for instance, useful to refer to the islands which lie in the eastern North Atlantic off the coasts of north-west Africa and Europe, namely the Azores, the Canaries, Madeira and the Cape Verdes, by the inclusive title of Macaronesia.




A more difficult case is that of the islands off the east coast of tropical Africa, which are sometimes called the East African Islands. They comprise Madagascar, the Comoros, the Aldabra Islands, the Mascarenes and the Seychelles, and there is no general term to cover them all. In the following pages the term "Madagascar, etc." is used for this purpose, and unless qualified may be taken to include the whole series of groups.

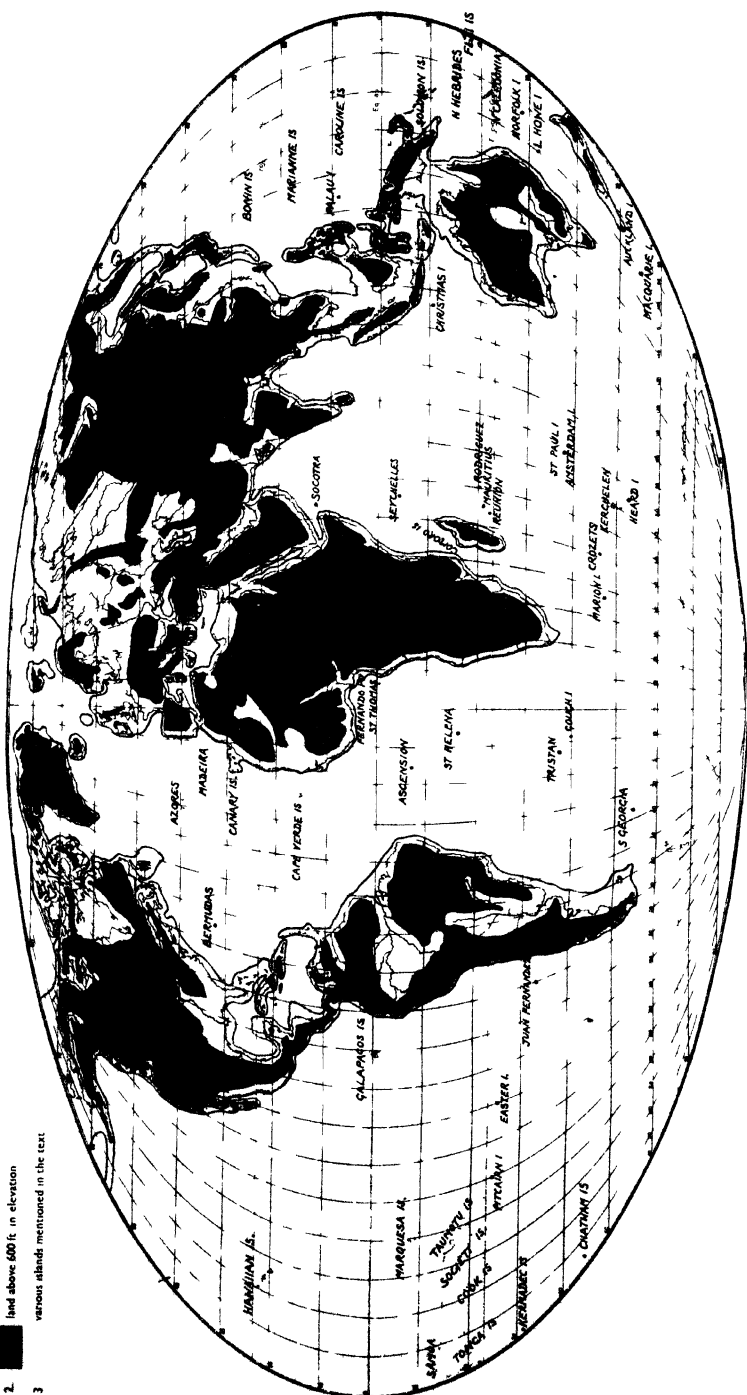
Australasia, again, is a very common term, but one with some ambiguity. Here it is used to mean Australia, New Zealand and its satellite islands, and, generally, New Caledonia, the Lord Howe and Norfolk Islands in addition.

The term Malaya is also sometimes open to misconception. Here it is used to include, not only the Malay Peninsula, but also the Archipelago, and it thus covers all the land between Burma, Siam and Australia.

Finally, the phrase "the Pacific Islands" is used to denote some or all of the islands north and east of the Malayan Archipelago and Australasia (as just defined).

PLATE 3

1.  the 600 ft submarine contour
2.  land above 600 ft in elevation
3.  various islands mentioned in the



Areas covered: Discussion increasing towards London
Approximate Scale 100 000 000 1600 miles in a square
on Mollweides Homolographic Projection

CHAPTER 2

THE DIVISION OF THE WORLD INTO FLORISTIC REGIONS

Major Zonations

THE major and most obvious segregation of the plant life of the world to-day is into three latitudinal zones—polar, temperate and tropical. These, owing to the shape of the earth and its position in relation to the sun are symmetrical about the equator. For most practical botanical purposes, however, this zonation is scarcely detailed enough and it is usual to incorporate a fourth zone and to speak of arctic (polar), temperate, subtropical and tropical zones.

A still fuller and more scientific classification is that quoted by Hansen (112), for example, which is as follows :

- | | | | | | | | | |
|------------------------|---|-----------|---------------------------------------|---|---|---|---|---|
| 1. Equatorial zone | . | 0·0–15·0 | degrees on either side of the equator | | | | | |
| 2. Tropical zone | . | 15·0–23·5 | " | " | " | " | " | " |
| 3. Subtropical zone | . | 23·5–34·0 | " | " | " | " | " | " |
| 4. Warm temperate zone | . | 34·0–45·0 | " | " | " | " | " | " |
| 5. Cold temperate zone | . | 45·0–58·0 | " | " | " | " | " | " |
| 6. Subarctic zone | . | 58·0–66·5 | " | " | " | " | " | " |
| 7. Arctic zone | . | 66·5–72·0 | " | " | " | " | " | " |
| 8. Polar zone | . | 72·0 | | | | | | |

This would be a satisfactory and accurate indication of the major distribution of plants were it not that it ignores one factor which actually complicates it very much. This is the influence of the elevation of the land.

It is well known that at any latitude a sufficient vertical rise from sea level epitomises in a very short distance the climatic zonation which is to be observed at sea level between the latitude in question and the nearer pole. Since climate and vegetation are in general very closely correlated, it follows that a vertical rise similarly epitomises the botanical changes which are to be observed at sea level between the latitude in question and the nearer pole.

This is illustrated by the familiar fact that as one ascends a mountain the plant life changes with increase in elevation until, if the rise is sufficient, a condition characteristic of polar latitudes is reached, so that the highest mountains, even if on the equator, have permanent ice and snow at their summits.

The vegetational zonation of mountains, and especially of tropical mountains, has been much studied and has been described and expressed in a number of classifications. The following, which is a combination of several, is a fairly familiar one.

On a high mountain situated in the more equatorial parts of the tropical zone in the old world, for instance, the lowest levels, namely those between sea and 600 metres, are occupied by a truly equatorial vegetation characterised by palms and bananas ; above them comes a tropical but less equatorial kind of vegetation in which tree-ferns and figs are prominent ; above this is a zone of subtropical types like myrtles and laurels ; above them another warm temperate zone of

evergreen trees ; next a zone of deciduous trees such as are familiar in temperate regions ; then a zone of coniferous trees ; then a zone of alpine shrubs ; and finally a zone of alpine herbs. Above this there is no appreciable vegetation.

This zonation may be summarised with figures as follows :

0- 600 metres	Zone of palms and bananas
600-1,250 "	tree-ferns and figs
1,250-1,900 "	myrtles and laurels
1,900-2,600 "	evergreen trees
2,600-3,200 "	deciduous trees
3,200-3,800 "	coniferous trees
3,800-4,450 "	alpine shrubs
4,450-5,050 "	alpine herbs
5,050- "	Permanent ice and snow ✓

Another and more extensive presentation of this zonation is illustrated in fig. 1.

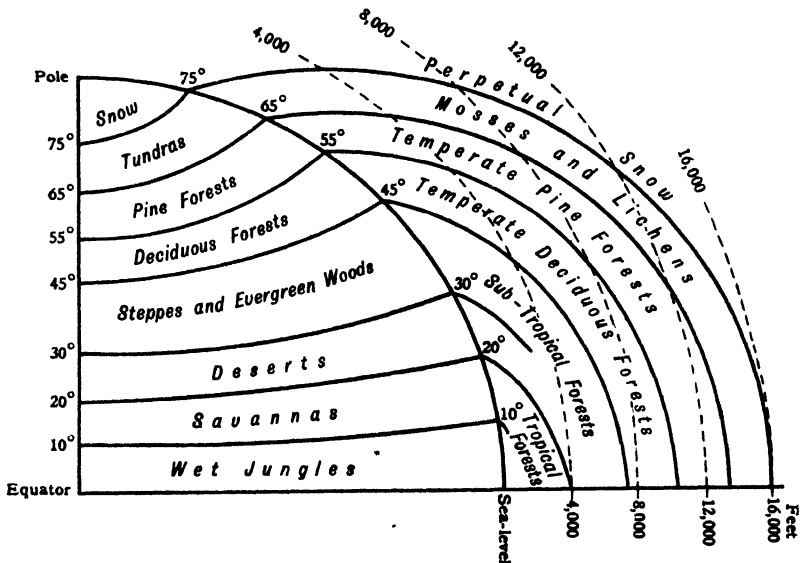


FIG. 1.—Diagrammatic representation of the vegetation zones of latitude and altitude.
(Redrawn from Herbertson's *Outlines of Physiography*, Edward Arnold & Co.).

It follows from what has been said that unless the relief of the land is very slight, each latitudinal zone of the world will afford suitable conditions for the appearance of plants in general characteristic of a zone or zones in higher latitudes. Subtropical plants will occur here and there in the tropical regions according to the relief: temperate plants will occur in both subtropical and tropical zones, and so on. If the elevation is sufficient, each type of plant or vegetation will find a congenial home somewhere at all latitudes nearer the equator.

From this there is to be drawn the very important conclusion that in no

latitudinal zone is the total land area exclusively available for the type of vegetation characteristic of the lowest levels in that zone. Some of it will be occupied by vegetation characteristic of the lowest levels of zones nearer the poles.

Detailed tables of figures relating to this interesting generalisation are given in Appendix A, but the two chief conclusions to which they lead may be summarised here.

The first relates to the absolute areas of the land occupied by the different kinds of vegetation on each side of the equator, and the figures show these to be, in thousands of square miles :

	<i>No Vegetation.</i>	<i>Arctic Alpine.</i>	<i>Temperate.</i>	<i>Subtropical.</i>	<i>Tropical.</i>
North hemisphere .	2,658	9,065	11,137	8,673	6,571
South hemisphere .	155	436	1,317	5,849	5,571
add Antarctica					

The second series of figures relates to the proportion of each of the climatic zones available for the different types of vegetation. Taking the corresponding zones in the two hemispheres together, and using a somewhat simplified phraseology, the figures are :

1. In the tropics only about 77 per cent. of the total land is occupied by tropical vegetation ; 17·5 per cent. is occupied by subtropical plants ; 4 per cent. by temperate plants ; and 1·5 per cent. by arctic alpine plants.

2. In the subtropics only about 67·5 per cent. of the total is occupied by subtropical vegetation ; 17 per cent. is occupied by temperate plants ; and 9 per cent. by arctic alpine plants.

3. In the temperate regions only about 74 per cent. of the total is occupied by temperate vegetation ; 18·5 per cent. is occupied by arctic alpine plants.

The residue of each zone is too elevated to bear flowering plants.

Further Classification

The average range of species is comparatively small. No doubt a laborious computation could be made to give a fair idea of the actual dimensions involved, but in the absence of any such figure it is enough to say that the area occupied by any one of the vast majority of species (and, it may be added, of most genera also) is far less than that of any one latitudinal zone. As a result of this the species present in one part of a zone are to a greater or lesser extent different from those in other parts of the same zone. Many factors help to determine the degree of this difference, and since these factors themselves show no regularity or constancy, it may be larger or smaller, so that the extent of geographical separation between two floras cannot alone be taken as a measure of the differences between them. Other means of estimation must be sought.

From this it is also clear that the plant life of the world can be classified geographically, not only on a vegetational basis, but also floristically, that is, into distinct floras, and a classification of this kind is an important adjunct to plant geography. It is, however, not easy to make because of the absence of any ready means of estimating floristic differences and relationships.

The situation may be made clear by an illustration. Take the case of a botanist familiar with the British flora, who for the first time visits North America. There he will find many plants which he has not encountered before, but for the most part they will be so like those with which he is acquainted at home that he will be able to identify them fairly easily. If the same botanist now visits New Zealand he will again find many unfamiliar plants, indeed even more, but on this occasion his previous experiences will be of little or no help in diagnosing them. In short, the difference between the floras of the British Isles and New Zealand are greater than those between the floras of the British Isles and North America. This is clear enough, but the difficulty is to put an absolute value on these differences and to compare them with others, as for instance those between the floras of North America and New Zealand.

Actually the fact that species are not equally closely related to one another makes it almost impossible to measure floristic resemblances and differences, and all that can be done is to utilise such evidences as may be available (and these are more often than not imponderable and intangible) to make what can be no more than a rough estimate. Of these possibilities the evidence based upon the endemic or peculiar elements of a flora is perhaps the most fruitful, but even this has a strictly limited value. To know, for instance, that half the species of any particular flora are peculiar to it, is often of interest and value, but more than one flora may show a similar degree of endemism and the statement affords no indication of the relationship between them. Indeed, expressions based on endemism serve really only to show how distinct from all others any one flora may be and help little in deciding closeness of affinity. Nevertheless, figures relating to endemism are useful and are frequently quoted in later chapters.

Again it is necessary in making a floristic classification to estimate the relative importance of different floras, and here too endemism can be of only minor assistance. There are other difficulties which it does not touch such as deciding the comparative values of the floras of two regions of very different size or of two floras of which one is large and the other small. How, for instance, is the flora of St. Helena, with perhaps under 100 species, to be compared with that of all Brazil, with many thousands of species? Yet both have the same degree of endemism. Must they on this account receive equality of status?

There are many such questions, and the region of the Pacific is particularly difficult in this way because of the great mutual isolation and tiny area of most of the land surfaces. In the classification given later one possible treatment has been adopted as being the most reasonable and useful, but others might be put forward. In connection with this particular part of the world it may be apposite to say here that there is reason to think that it may hold the key to many phytogeographical problems, and for this reason it is an area of special importance that has received much study. Two particularly useful general references are to papers by Skottsberg (225) and Guillaumin (105).

But the difficulties need not be further stressed and in spite of them many floristic classifications have been made, one of the earliest and most illustrative of these being by Schouw in 1823. This is quoted below rather fully, not only for its intrinsic value as a forerunner of modern systems, but because it shows the character that may be imparted to a region by the strong development therein of particular plant groups (211).

Schouw divides the world into 25 kingdoms, naming them, wherever possible, after the most characteristic plants, as follows :

1. Kingdom of saxifrages and mosses. Alpine arctic.
 - a. Province of sedges. Arctic.
 - b. Province of Primulaceae. Eurasian alps.
 - c. Province of shrubby alpine Composites. American alpine.
2. Kingdom of Umbelliferae and Cruciferae. North Eurasia.
 - a. Province of Cichoriaceae. North Europe.
 - b. Province of *Astragalus*, halophytes, thistles. North Asia.
3. Kingdom of Labiates and Caryophyllaceae. Mediterranean region.
 - a. Province of Cistaceae. Spain and Portugal.
 - b. Province of *Scabiosa* and *Salvia*. South France, Italy and Sicily
 - c. Province of shrubby Labiates. Eastern Mediterranean.
 - d. Province of North Africa.
 - e. Province of *Sempervivum*. North African Islands and Morocco.
4. Kingdom of *Aster* and *Solidago*. Northern North America.
5. Kingdom of Magnolias. Southern North America.
6. Kingdom of Camellias and Celastraceae. China and Japan.
7. Kingdom of Scitamineae. India.
8. Kingdom of the Himalayas.
9. Kingdom of Polynesia.
10. Kingdom of the Malayan Mountains.
11. Kingdom of Oceania.
12. Kingdom of balm trees. South-west Arabia.
13. Kingdom of deserts. North Africa and North Arabia.
14. Kingdom of Tropical Africa.
15. Kingdom of Cactaceae and Piperaceae. Central America and Northern Tropical South America.
16. Kingdom of the Mexican mountains.
16. Kingdom of *Cinchona*. Northern Andes, lower levels.
18. Kingdom of *Escallonia* and *Calceolaria*. Northern Andes, higher levels.
19. Kingdom of the West Indies.
20. Kingdom of palms and Melastomataceae. Eastern tropical South America.
21. Kingdom of woody Composites. Middle Andes.
22. Kingdom of Antarctica. Patagonia, Fuegia and Falklands.
23. Kingdom of *Stapelia* and *Mesembryanthemum*. Extra-tropical South Africa.
24. Kingdom of *Eucalyptus* and Epacridaceae. Extra-tropical Australia.
25. Kingdom of New Zealand.

It is remarkable that at such an early date so complete a classification should have been made. It is naturally open to much criticism in the light of modern knowledge, but its imperfections and incompleteness are largely due to the lack of knowledge of its time. In many respects it compares favourably with much more modern schemes.

Prominent among these latter is the original scheme of Engler (71) and its various derivatives, but no one of them is suitable for all and every purpose. Especially is there none particularly adapted to the practical requirements of this book, and the writer has therefore ventured to compile a special classification for the purpose of providing a framework within which the subject matter of the next few chapters may appropriately be arranged. It must be emphasised that this classification has been drawn up solely on the score of immediate convenience, and although it is based on some of the best-known schemes it will not necessarily prove equally suitable for other purposes.

This classification divides the floras and floristic units of the world first into

kingdoms, then into regions (this being the category of chief importance), and finally into provinces, and is as follows :

CLASSIFICATION OF THE WORLD INTO FLORISTIC UNITS

(Plate 4)

BOREAL KINGDOM :

- a. Arctic and Sub-arctic Region
 1. Eurasian province
 2. Greenland
 3. Nearctic
- b. Euro-Siberian Region
 1. Western Europe
 2. Central Europe
 3. Scandinavia
 4. Russia
 5. Danube basin
 6. European alpine
 7. Caucasus
 8. Western Siberia
 9. Altai—Trans-Baikalia
 10. North-eastern Siberia
 11. Kamchatka
- c. Sino-Japanese Region
 1. Manchuria and South-eastern Siberia
 2. North China
 3. North Japan
 4. West China
 5. South China
 6. South Japan and Korea
 7. Sino-Himalayan-Tibetan mountains
- d. Western and Central Asiatic Region
 1. Armenian-Persian highlands
- e. Mediterranean Region
 1. Lusitania
 2. Eastern North Mediterranean coasts
 3. Morocco—Tunis
 4. North Egypt and Syria
- f. Macaronesian Transition Region
 1. The Azores
 2. Madeira
 3. The Canaries
 4. The Cape Verdes
- g. Atlantic North American Region
 1. Canadian Conifer province
 2. The Great Lakes
 3. The Appalachians
 4. The Prairies
 5. Atlantic and Gulf coasts
 6. Mississippi basin
- h. Pacific North American Region
 1. Sitka and British Columbia
 2. California
 3. Rocky Mountains
 4. The Great Basin
 5. Sierra Nevada
 6. Montane Mexico

PALAEOTROPICAL KINGDOM :

A. African sub-kingdom—

- a. North African—Indian Desert Region
 1. Sahara—North and Central Arabia
 2. Mesopotamia
 3. Persia—North-west India
- b. Sudanese Park Steppe Region
 1. Senegambia—Sudan
 2. Upper Nile-land
- c. North-east African Highland and Steppe Region
 1. Abyssinia and Eritrea
 2. Galaland and Somaliland
 3. Yemen and South Arabia
 4. Socotra
- d. West African Rain - forest Region
 1. Upper Guinea
 2. Cameroons etc.
 3. Congo basin
 4. Central Africa
 5. Northern Angola
- e. East African Steppe Region
 1. The Zanzibar coast
 2. The Mozambique coast
 3. Southern Portuguese East Africa
 4. The East African high mountains

A. African sub-kingdom—*cont.*

5. The Central African lake zone
6. Nyasaland
7. Bangweulu-Katanga
8. Northern Rhodesia
9. Southern Rhodesia
10. Southern Angola and Northern South West Africa

f. South African Transition Region

1. High veldt of the O.F.S. and Transvaal

2. The Kalahari
3. The Karroo
4. Namaqualand and Damaraland
5. Natal and eastern Cape Province

g. East African Island Region

1. Madagascar and the Comoros
2. The Seychelles
3. The Mascarenes

h. Region of Ascension and St. Helena

B. Indo-Malayan sub-kingdom—

a. Indian Region

1. Malabar coast
2. Deccan
3. Ganges Plain
4. Tropical flanks of the Himalayas
5. Assam and Upper Burma
6. Ceylon

b. Continental South-east Asiatic Region

1. Lower Burma

2. South China coast and Formosa
3. Siam and Annam
4. The Malay Peninsula

c. Region of the Malayan Archipelago

1. Java, Sumatra and the Sunda Islands
2. Borneo
3. Celebes and Moluccas
4. New Guinea
5. Philippines

C. Polynesian sub-kingdom—

a. Hawaiian Region

b. Region of New Caledonia (with the Lord Howe and Norfolk Islands)

c. Region of Melanesia and Micronesia

d. Region of Polynesia

NEOTROPICAL KINGDOM:

a. Caribbean Region

1. Mexican xerophyte province
2. Mexican lowlands and coast
3. South Florida, West Indies and Bermudas
4. Guatemala—Panama
5. North Colombia and North Venezuela

b. Region of Venezuela and Guiana

c. Brazilian Region

1. Hylaea
2. Eastern coasts

3. Uplands of Central Brazil

4. Highlands of Eastern Brazil

5. Grand Chaco

d. Andine Region

1. Tropical and subtropical flanks of the Andes
2. Atacama desert etc.
3. Chilean sclerophyll zone
4. Montane Andes
5. The Galapagos Islands

e. Pampas Region

f. Region of Juan Fernandez

SOUTH AFRICAN KINGDOM:

a. Cape Region

AUSTRALIAN KINGDOM :

a. North and East Australian Region

1. Northern forests
2. Queensland forests
3. South-eastern forests
4. Tasmania

b. South-west Australian Region

- c.* Central Australian Region
 1. North and east savannahs
 2. Central deserts
 3. South Australia

ANTARCTIC KINGDOM :

a. New Zealand Region

1. Tropical New Zealand
2. Temperate New Zealand
3. New Zealand Alps
4. Kermadec Islands
5. Chatham Islands
6. Auckland and Campbell Islands

b. Patagonian Region

1. Patagonia
2. Southern Andes
3. Falkland Islands

c. Region of the South Temperate Oceanic Islands

This floristic classification may be epitomised (as it is convenient to do for many immediate practical purposes) by saying that it divides the land surfaces of the world into 36 regions, the floras of which may, for theoretical purposes, be regarded as roughly equivalent in value, though not of course in size nor, necessarily, in interest.

Where convenient and appropriate the subject matter of later chapters will be arranged under the headings of these regions, and details concerning them will be noticed as occasion demands. It must be pointed out, however, that the Euro-Siberian region is much more extensive, in longitude at least, than any of the others. To divide it reasonably is difficult, and to do so would upset the balance of the list, and it must therefore be left as it is. Its exceptional dimensions will, however, make it necessary to treat it later as a rather special case.

CHAPTER 3

SOME GENERAL ASPECTS OF PLANT GEOGRAPHY

✓ The Evolutionary Background

THE short history of the study of plant geography in the Introduction is enough to show the enormous influence that evolutionary conceptions have had on the development of the subject, and it is no exaggeration to say that its whole background has become an evolutionary one. Evolution is, as it were, the medium in which the picture of plant distribution is painted.

All the latter part of this book is devoted to a consideration of what are usually called the factors of distribution, that is to say the influences which may be looked upon as the immediate causes of the observed facts, but it will be clear from what has just been said that all these, critical as they may be, are to be regarded as secondary. Behind and beyond them is the infinitely broader cause inherent in the nature and course of organic evolution in general and of plant evolution in particular. Whatever the more precise explanation of them, the facts themselves are primarily due to something innate in the very order of nature. This something is the ubiquitous periodic production of new forms (species, genera and families) by the processes of evolution. This is the general theme of which the so-called factors of distribution provide the variations.

Clearly then the study of plant geography must be approached with this evolutionary conception in mind, and such an approach at once reveals two of the most fundamental features of the subject.

The first is that plant geography must always be regarded as a developmental study, and as dynamic rather than static. Whatever the particular facts under discussion it must always be remembered that they are not isolated and unrelated facts, but the culmination of a long series of events and changes which have been in operation at least for some time and often for very long periods. They are the outcome of that gradual change which is the essential feature of evolution, and if they are to be understood properly due account must be taken of the past as well as of the present.

Second, it is manifest that time must always be one of the most important factors in all aspects of plant geography. Evolution is generally visualised as a continuous, though perhaps unevenly continuous, process and one in which the state of affairs is constantly changing, so that, in theory at any rate, the constitution and distribution of the world's plant life can only be described in relation to time itself, and it must not be assumed without other evidence that the circumstances controlling plant distribution to-day are necessarily those which have controlled it in the past.

The central problem of evolution has always been that of the methods by which new and distinct forms arise, that is to say of the processes involved in the "origin of species." It would be inappropriate, if nothing more, to discuss this huge subject at any length here, but it is also impossible to neglect it altogether because of its bearing upon a question to which, before commencing the study of plant geography, an answer is an urgent necessity.

This is the question of whether a species originates once and once only in the course of evolution or whether one and the same form may arise more than once at intervals of space and time. To give the problem greater definition, species may be said to consist of a number of closely similar individuals. Are these individuals all to be regarded as directly descended from a single and comparatively recent ancestor, that is to say as being *monophyletic*? Or are they to be regarded as having originated, some by one line of descent in one place and others by different lines elsewhere, that is to say as being *polyphyletic*? Is it, in short, safe to assume that all the individuals comprising a species are blood relations, or is it more likely that mere superficial resemblance is the chief bond between them?

A moment's reflection will show the importance of this question to the plant geographer. If a species is strictly monophyletic, then all its individuals are the descendants of one and the same ancestral plant and their total range, however extensive and peculiar it may be, must have grown by the processes of dissemination from the tiny area occupied by this ancestor. However wide may be the space between two or more individuals, this space must be the consequence of progressive geographical divergence in the course of time.

If, on the other hand, a species is polyphyletic, then most of the features of its geography, however striking they may be, lose much of their interest and become almost meaningless and inexplicable, since there is nothing to show and no reason to suppose that the positional relationship between the individuals is anything but fortuitous.

In view of this it is obviously imperative before going further to come to some conclusion on this matter, and since this cannot be done without some reference to the subject of evolution in general and its theories, no further justification need be sought for making such a digression here.

Evolution is the natural antithesis of the conception of "special creation," which was the previously accepted explanation of the facts revealed by the study of animal and plant classification. Darwin (52), therefore, when he first propounded his views on evolution, was at some pains to do so in such form as would demonstrate, in the most telling fashion, the inadequacy of special creation as an explanation of the facts. He was also under the necessity of outlining some mechanism by which evolution might be supposed to come about, since without this his views would have been little more than academic. To meet these requirements he postulated his theory that evolution was brought about by "natural selection by survival of the fittest." The facts upon which he based this hypothesis were those of variation, the observed circumstance that no two individuals, even if of the same parentage, are ever exactly alike. He suggested that some of these differences would confer on their possessors advantages in the struggle of life, while others would be detrimental, and that since, as Malthus (155) had already shown, not all the individuals born can hope to survive, those best equipped would tend to be selected. This process he envisaged as accumulating with the passing of generations until some individuals had become sufficiently different from their earlier ancestors to merit recognition and description as new species.

There was nothing in the conception of special creation to preclude the possibility that similar individuals might have been created more than once and in different places, and in order to support his evolutionary views Darwin therefore devoted considerable time and space to an attempt to demonstrate that the weight

of evidence was in favour of the opposite view, and that species were in fact normally monophyletic rather than polyphyletic.

It was moreover important to do this from the point of view of the details of the suggested process of natural selection because, if this is indeed the mechanism of evolution, it is almost impossible to imagine that species can be anything but monophyletic. The chances that natural selection will, in two different parts of the world or at different periods, lead to exactly the same morphological result, can only be regarded as most improbable.

Perhaps on much the same grounds, Darwin and his contemporaries did not attach much importance to sudden and comparatively large evolutionary changes, but concentrated upon what are generally called "infinitesimal variations." If there is no theoretical limit to the magnitude of evolutionary change there must be visualised the possibility of some new form, widely different from anything hitherto existing, arising quite suddenly and unheralded, and there would be considerable difficulty in divorcing this kind of origin from the suggestion of an act of special creation. It was all-important rather, to show that evolution was an orderly process as opposed to the condition of arbitrariness, which must in one sense at least be inherent in the conception of special creation.

But it was also actually from the point of view of plant geography that Darwin saw the importance of demonstrating the monophyletic origin of species. As he himself expresses the point in the *Origin of Species*—"If the difficulties be not insuperable in admitting that in the long course of time all individuals of the same species belonging to the same genus have proceeded from one source, then all the grand leading facts of geographical distribution are explained on the theory of migration, together with subsequent modification and the multiplication of new forms." That is to say, given a monophyletic origin of species, the facts of plant and animal geography afford useful evidence in support of the theory of evolution.

It is for such reasons as these that the present-day reader of the works of Darwin and his contemporaries is often impressed with the extreme importance which is paid to minute variations and to the establishment of a general belief in the monophyletic origin of species, an importance which in the light of modern knowledge seems exaggerated. It seems so, however, only because the views that it seeks to establish have in fact been implicitly if not explicitly accepted by biologists for many years, and because it is difficult to realise, in the light of after-knowledge, how essential it was to establish them.

It might therefore be deemed justifiable to accept these opinions as a general premise to a consideration of plant geography without more discussion, but the state of biological knowledge has advanced enormously since Darwin's time and it is necessary to be satisfied as to how far, if at all, these views now require modification (248).

At the time when Darwin was writing his classics, knowledge concerning the cell and its structures was slight. It was but comparatively recently that the nucleus had been discovered and nothing was known of its internal organisation. Moreover, the work of Mendel on inheritance had still to be discovered by the scientific world. At this time, therefore, the evolutionist was unavoidably at a grave disadvantage because whatever mechanism he might suggest as being the vehicle of evolution, it was impossible to suggest any structural features in the living organism which might be the physical expression of it. Darwin fully

realised this difficulty and indeed found it necessary later to augment his original exposition of Natural Selection by the additional hypothesis of "pangenesis" in which he tried to picture how reproductive cells might be capable of transmitting characters to their progeny. Incidentally it is no small measure of Darwin's greatness that his guesses in this matter have very largely been substantiated, though not exactly in the terms he employed.

It was partly due to this difficulty that while evolution as a general theory became widely accepted, a mechanism which stressed the importance of small variations was less acceptable. Indeed there gradually grew up the view that evolution proceeded rather as a result of larger and more sudden changes, called mutations (54). Such large changes were observed in many plants and it was found that their occurrence could be accelerated by certain experimental methods, but the mutationists were at first in much the same difficulty as Darwin because of their ignorance of cytology and genetics.

The enormous advances which have been made in these two subjects since the beginning of this century now enable a more scientific view to be taken of these apparently antagonistic opinions and it is clear that they are far less opposed than was originally thought, this conclusion being in great part the fruit of the remarkable investigations that have been made into the microscopic structure of the cell-nucleus.

It is now known that the inheritance of characters between parent and offspring is by the agency of the chromosomes, which constitute the essential part of all cell nuclei. There is, moreover, every reason to believe that these characters are actually resident on the chromosomes in or as entities which are called *genes* and that alteration in transmissible characters is due to actual alterations of some kind in one or more genes. When an individual differs markedly from its forebears in an inheritable character it is generally believed that this difference originates as a definitive change in the nature or potentiality of one or more genes.

At first sight this "theory of the gene," as it is called, seems strongly to support the views of the mutationists, in as much as it puts into the general category of mutations all changes in characters since these must, by the nature of the case, be sudden and more or less sharply defined. But this is not quite a fair statement of the position. There are no particular limits in either direction to the magnitude of changes. Some may be large, but others are very small, and indeed are only to be compared with such minute modifications as were comprehended by Darwin in the phrase "infinitesimal variations." The fact of the matter appears to be that gene changes may be of almost any magnitude. If they are large, then they result in what is normally called a mutation: if they are small, they cause no more than minor variations. The distinction between them is primarily one of degree only.

The last forty years or so have also seen the accumulation of a vast amount of knowledge concerning the laws and phenomena of Mendelian inheritance, by which are determined the ways in which the characters possessed by parents are distributed among and expressed in their offspring. Here, again, there is more than one circumstance which may lead to the sudden and unexpected appearance of a form appreciably unlike any of its immediate ancestors which may in favourable conditions be the origin of a new species or at least of a new line of descent.

In brief it may be said that at the present time it seems that the new morpho-

logical forms which are the basis of the recognition of new species arise chiefly, and possibly exclusively, from one or other of the following processes :

1. By gene mutation.
2. By segregation of characters according to the laws of Mendelian inheritance.
3. By hybridisation, namely the breeding together of relatively unlike parents (180).
4. By changes in the number of chromosomes and genes (276).

It is impossible to go into details of these processes here, and those who wish to know more about them may refer to Cain (276) and to standard text-books on cytology and genetics, but it will be seen at once that they do not include the "accumulation of small variations" by which natural selection was presumed to operate, and therefore that this, if it exists at all, is believed now to play no more than a minor part in the origin of species. This is very important because it is the one evolutionary process which would, as has been explained, almost inevitably lead to species being monophyletic.

On the other hand, these modern ideas on the origin of species do not increase the likelihood of polyphyletic in its usual sense of the derivation of similar forms from unlike ancestors. They do, however, greatly increase the likelihood of the same form being produced, from the same parent stock, more than once and at different places within its area. This newer conception is conveniently distinguished from polyphyletic descent in its older sense by the terms polytopic and polychronic, which are applied respectively to forms arising at more than one spot and at more than one time.

At first sight these ideas may seem likely to add a great complexity to plant geography, but in practice this is not likely to be serious. In the first place, for reasons which may be deduced from what is said elsewhere in this book, the areas over which polytopy may occur are not likely to be great, nor is the period of polychrony likely to be very long. In the second place there is reason to suppose that gene mutations and changes in chromosome number are, in nature, often induced by environmental factors. These themselves will tend to vary considerably from place to place and from time to time and to produce appropriately dissimilar, rather than similar, effects.

To sum up—it appears that there is no reason in the light of modern developments to revise the generally held view that the truly polyphyletic origin of species is little more than a rather hypothetical contingency, for which the plant geographer need not make very serious allowance. At the same time there is good reason to believe that polytopy and polychrony may occur frequently in nature but that both these are of comparatively local effect and unlikely to confuse the general issue involved in the study of discontinuous and other major forms of distribution.

The Cycle of Distribution

The next question to be discussed is that of the geographical fate of species or genera after they have arisen by one or other of the processes of evolution mentioned above, and in accordance with the conclusions arrived at there we may assume that this origin has been monophyletic.

If the monophyletic origin of species be accepted in its most extreme form it must be believed that a new species, when it first appears, does so as one or very few individuals only. In this condition it may be described as having no distribution in space, but this will persist only until such time as the first generation produces

progeny. This stage is generally a very short one, for as soon as the species reproduces its range must increase if for no other reason than that no two plants can occupy exactly the same position. If the new species is biologically sound and able to maintain itself normally among pre-existing species it will tend to increase its range further, roughly in accordance with the number of its individuals. At some point or other various external factors tending to restrict its spread will almost inevitably come into play, but for a time at any rate it will continue to increase its range at each reproduction. This point may come soon, in which case the species will never be widespread, or it may be long delayed, in which case the species will rapidly attain a considerable range. In either case the first stage in its geographical history will be one of spread culminating in the attainment of an appropriate degree of distribution, and of an equilibrium in respect of associated species.

During this first stage, however, the processes of evolution are proceeding, and sooner or later the erstwhile new species will in turn produce fresh species. This it may do from individuals at any point of its range, or from individuals in certain parts of its area only, but whichever prevails the result will be that new specific distributions or ranges will arise within the area of the parent form or at least in close proximity to it.

There is good reason to believe that the life of a species has much the same course as the life of an individual, and that it passes fairly early through a stage at which it exhibits a maximum vitality. From a phyletic point of view this expresses itself in a maximum evolutionary activity, and hence we may characterise this second stage in its history at that at which it produces a maximum of new forms.

As time goes on this vitality will ebb or, to put it rather differently, will be passed on to succeeding generations and the original will gradually diminish and die out. It will pass in fact into what has been called a condition of incipient senility. Its powers of producing new forms will decrease or cease altogether and it will have greater and greater difficulty in maintaining itself against the competition of younger and more virile strains. This stage again may come soon or may be long delayed, but come it must, and the species will eventually die out altogether.

Concurrently, and with the consequent diminution in the number of its individuals, the range of the species will also tend to diminish until in the final stages both the plant and its range will disappear entirely.

From a geographical point of view this late stage is a very interesting one. Throughout its history the conditions in which the species exists are constantly changing through a variety of circumstances and it is likely, and indeed almost inevitable, that the disappearance of the species will be a differential disappearance, that is to say will take place first in one part or another of its range rather than everywhere simultaneously. Geographically the result of this will be a strong tendency towards the development of a discontinuous range, one indeed which will consist of two or more disjunctive constituent parts: Such ranges form one of the most intriguing subjects of plant geography, and since on the assumption of a monophyletic origin they can scarcely arise otherwise than has been outlined their significance as an indication of the state of the species showing them is very great.

Ultimately, and for a varying time before its complete disappearance, the species will have but a very restricted range. If earlier it was discontinuous the further

passage of time will see the gradual elimination of all but one of the constituent areas until eventually the range of the species returns to a condition comparable with that which it possessed at the earliest stage of its existence.

To summarise, it would seem therefore that the history of a species or genus and of its distribution will normally consist of four successive stages, each represented by a different and well-marked condition, and this view has been called the Theory of Generic Cycles.

The first stage may be called the juvenile stage, and during it the species is establishing itself and gradually extending its range from nothing to a maximum determined by various external conditions.

The second stage represents the maturity of the species. During this it will exhibit a maximum phyletic activity and give rise to various new forms, numerous or the reverse. It will meanwhile in general maintain its maximum range, within or associated with which there will appear the incipient ranges of many closely related younger forms. It will show indeed what may be described as a parental range inclosing a number of offspring ranges.

In the third stage the species is passing gradually into senility. It no longer produces many new forms and it is giving place to the newer and more virile generations. For a time it may maintain its range, but sooner or later this must tend to decrease. This decrease is likely to be accompanied by a breaking up of the range into disjunctive parts owing to the disappearance of the plants earlier in some places than in others.

The fourth and last stage marks the final disappearance of the species and the ultimate contraction of its range to vanishing point. As in the course of this extinction the range decreases, it approximates more and more closely in extent to that which the species possessed in the earliest stage of its career. Finally, for some time before final extinction the size of its range will be indistinguishable at sight from that of a species but newly formed.

It must not be supposed that all species follow exactly the same course in their development and decay, but there can be no doubt that this is a fair picture of their general prospects. The actual details will, however, obviously depend on many considerations. One or other of the stages may be unduly prolonged or much shortened; the length of them will always tend to be controlled by extraneous circumstances. Some species may never attain an appreciable range and may die out without showing either the second or third distributional stages. Others may early attain and long maintain a wide distribution. There is no doubt, too, that the matter of evolutionary vitality, as it has been termed, namely the ability to produce new forms, varies enormously not only among different kinds of plants but also in different circumstances and in different places (220), and it may well be that external changes may induce copious species production in forms which formerly gave rise to them but sparsely. It is difficult also to avoid the conclusion that certain parts of the world are peculiarly favourable for intense and rapid evolution.

Such are some at least of the kinds of complications which may and do obscure the simplicity of distribution. Were it not for these complications it would no doubt be possible to describe and explain plant geography much more concisely and completely than it is at present, but it would certainly be a far less interesting subject.

Endemism

To quote the *Concise Oxford Dictionary* the word *endemic* means "Regularly found among (specified) people, in (specified) country." That is to say, it is applied to things which are peculiar to a given situation.

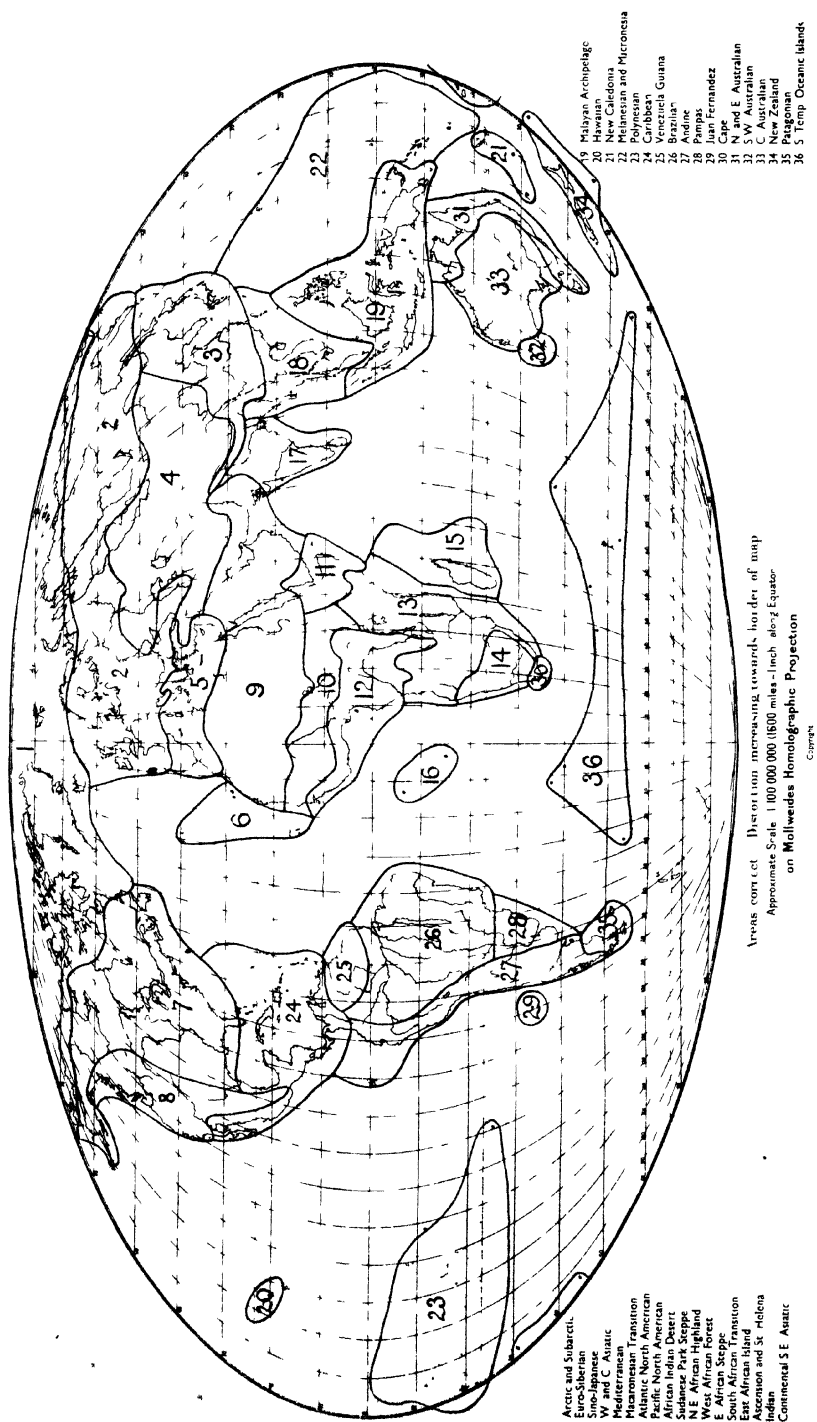
In botany the word *endemic* is applied to any species or other taxonomic unit which is so distributed as to be confined to one particular country or region. It will therefore be seen that without further qualification the word is almost meaningless because every species is confined to some area though it may be a very large one. In the geography of plants and animals, therefore, the use of the word is restricted somewhat conventionally to species or other units having a comparatively or abnormally restricted range. It should also properly be used with due regard for the size of the taxonomic unit under consideration. Although it is generally indescribable in words, there is an average range of families, an average range of genera, and an average range of species, these being progressively smaller, and the best practical limitation of the use of the word *endemic* is to restrict it to units whose ranges are obviously less than the average for their kind. For example, it is appropriate and valuable to consider families which are found in only one continent as *endemic* because the average distribution of families is probably greater than this. On the contrary it is almost meaningless to speak of species in terms of continental *endemism* because comparatively few species are as widely or more widely distributed. Areas beyond a certain size will always tend to have a large percentage of *endemic* species for the simple reason that the great majority of species have ranges of less than these dimensions.

At the same time it is difficult to lay down any hard and fast rules and all that can be done is to bear in mind the importance of denoting in some way the sense in which the term *endemism* is used. It may be desirable to use it in one set of circumstances and indefensible in others.

— It has already been explained that *endemism* may be particularly useful in the recognition of different floristic regions and also in determining or expressing the degree in which floras are peculiar. In the first case it is often to be noticed that while one part of a large region possesses a high proportion of *endemics* another and adjacent region may have considerably fewer, and this is often a useful guide to the delimitation of the two. This is seen, for instance, between the Cape Region and other parts of South Africa, and between south-west Australia and other parts of that continent.

The second case may be well illustrated by three island groups, the Galapagos, Juan Fernandez and Hawaii. The first has many *endemic* species but very few *endemic* genera, and even the *endemic* species are comparatively closely related to continental American types. Juan Fernandez is situated fairly close to Chile and has a small flora only, but this is very peculiar, its *endemics* including many genera and even one family. The Hawaiian Islands are very isolated and have a flora much larger than those of the other groups. Moreover, it has a very high degree of *endemism*, no fewer than some 90 per cent. of its species being confined to the archipelago. There are also many *endemic* genera.

Although the number of species in each of these floras is very different, the facts of *endemism* indicate clearly that the floras of Juan Fernandez and Hawaii have a much greater and more similar proportion of peculiarity than the Galapagos Islands. It is partly for this reason that, in the floristic



classification given in Chapter 2, a higher rank is given to the former than to the last.

It was made clear above that species and other units will of necessity be endemic in range at two distinct periods of their existence, namely at the beginning and the end, when they are very young and very old. In the first case they will be endemic because they will not have had time to spread more than a little way; in the second case they will be endemic because their ranges have become circumscribed almost to vanishing point. Thus it is obvious that endemism, in the sense of narrowness of range, is not necessarily an indication of the age of the unit exhibiting it (201, 202). Very young and very old species may show similar ranges. The realisation of this has been expressed in the practice of referring to "old" endemics as "relics," and they have actually been given the special name of "epibiotics."

Discontinuity

Discontinuity, or disjunction as it is sometimes called, is the occurrence of a species or other unit in two or more separated regions and is by no means an uncommon phenomenon. Sometimes the extent of discontinuity is very small and the range as a whole is almost continuous; sometimes the discontinuity is great and even to be measured in thousands of miles. Between these two extremes there is almost every intermediate condition.

In theory, of course, all species are discontinuous to some extent in so far as they rarely if ever cover their general range so completely that the individual plants are actually in contact, and the greater the detail in which distribution is considered the more apparent this point of view will become. In general, however, and especially in considering the whole ranges of species and genera, it is impossible to take into account, or indeed to mark, this degree of discontinuity, and the term is restricted in practice to ranges which on a large and obvious scale consist of two or more parts. Even so the term remains comparative and this must always be remembered, and in reference to it the degree of discontinuity comprehended should if possible be stated explicitly.

Discontinuity is closely related to two matters which have already been mentioned in this chapter. The first is the problem of the monophyletic origin of species. If this view is maintained, then obviously the phenomena of discontinuity take on a very great interest and importance because it may be assumed that whatever is the present separation between the constituent areas they must once have been continuous, or at least the individuals contained in them must once have come from one ancestral plant.

This being so, then the discontinuity has to be explained, and there must be taken into account all the factors which might possibly have caused it, and this often leads the investigator into fascinating by-ways of his subject.

On the other hand, if species are polyphyletic then discontinuity loses much of its potential importance because it can always be explained on the supposition that the same species has arisen independently in each of the separated portions of its total range.

As has been said, discontinuity is quite common, and appears in all sorts of forms, and it is unlikely that any serious critic would be found to maintain that all and every of its examples are due to the species concerned having had a polyphyletic origin. On the contrary, the detailed facts are generally such as to

indicate very strongly that this is not the case and that discontinuity is the result of real disjunction.

Discontinuity is also closely related to the Theory of Generic Cycles outlined above and will be seen from it to be in some form or other an almost inevitable concomitant of the phase of senility. Hence discontinuity is only to be expected and is to be regarded as a normal phenomenon of distribution. It is of course affected, like the other phases, by all kinds of extraneous causes and extreme discontinuity is no doubt to some extent abnormal, since it can arise only in definite circumstances. It is for this very reason of special interest and importance, especially from a theoretical point of view.

Actually the present geography of the world is such that any unit with an extended range must of necessity be discontinuous. Even northern circumpolar ranges are broken by the gaps of the north Atlantic and the north Pacific, and the increasing segregation of land makes this more and more noticeable the further south we go from the North Pole. The tropical region, for example, is divided by oceans into three main masses corresponding to the continents, while the same kind of segregation is seen even more markedly in the southern temperate latitudes. Hence all the plants which range completely over at least one major climatic world belt must be discontinuous in total distribution. Clearly, to include these under the consideration of discontinuity would make for complexity, and therefore it is a working convention that by discontinuity is meant only such disjunction as is, so to speak, over and above that due to major land and sea distribution. For example, units which are pan-tropical in range are not usually considered or treated as discontinuous. Their ranges are in fact of necessity discontinuous, but this is not their primary interest. On the other hand, units which are found only in certain parts of the tropics separated by areas of ocean are so considered.

It is also apparent that discontinuity can be water discontinuity, land discontinuity (where a unit is irregularly distributed over a large land surface), or a mixture of both. Each kind involves rather a different combination of considerations and in theoretical matters the distinction between them should not be lost.

✓ Age and Area

At the beginning of this chapter it was emphasised that time must always be a potent factor in plant distribution, and those who have read the preceding pages, and especially those dealing with the cycle of distribution, may have gained the impression that the areas of species will sometimes be a measure of the length of time that they have existed. Actually this has long been something of an axiom of plant geography and it is implicit even in such early writings as those of Hooker in the middle of last century.

This conception, that the longer a species has existed the greater will be its area of distribution, has been moulded by Willis (262) into a very detailed hypothesis of plant geography under the name of the Theory of Age and Area. About this theory, which has excited much interest and comment, there has been much controversy, and no general account of plant distribution can be complete without some attempt to give a reasoned appreciation of it.

That age and area may be, and in individual cases no doubt frequently are, closely related, is beyond question, and it would be difficult to find anyone

prepared to deny this totally. There are, however, great differences of opinion as to the extent to which it is true in fact, and it is on this point and not on the broad conception that Willis' theory has proved contentious.

Two aspects of the presentation of the theory tended to increase the opportunities for disagreement. Instead of making, without qualification, a comparatively simple and limited postulation, Willis tried to make the theory too wide and was obliged to incorporate in the statement of it a number of troublesome reservations, of which his critics were not slow to avail themselves.

He also sought to support his views by the aid of somewhat abstruse statistical studies and the graphs and curves resulting from them. In particular he showed that many facts of distribution were expressed by a peculiar kind of graphic curve which he and his collaborators called a "hollow curve," and he maintained that this type of curve was characteristic of the conception of age and area and evidence of its truth.

Unfortunately this mathematical treatment did not enhance his theory. The real meaning and significance of the "hollow curve" was problematical, and it was soon shown that similar curves could be obtained from many sources unconnected with plant distribution. Moreover, many botanists found it very difficult to understand the curves, and there was almost inevitably imparted to the theory an air of mystery that was unfortunate. Many felt that if the theory was really sound it should not be dependent on this rather incomprehensible kind of evidence.

In addition Willis made it clear that in his opinion one great value of his theory was that it afforded a point of view in opposition to the theory of natural selection, and he associated it closely with the alternative hypothesis of Differentiation (see below).

To-day sufficient time has elapsed to permit a reasonably final valuation of Willis' theory. The idea of a relationship between age and area is undoubtedly true in theory, but there is equally little doubt that in practice it is, owing to all manner of complicating circumstances, much less widely applicable than Willis maintained. Indeed it could only be of general application if it could be imagined that the circumstances in which evolution has proceeded have been uniform for vast periods of time, and this almost every aspect of plant geography disproves. It has therefore been said with some truth that the theory is no more than a well-known axiom in disguise, namely that if two species with the same potentiality of movement begin to move at different times the earlier starter will at any one future time have extended further than the other. This criticism is perhaps over severe, but it is nevertheless extremely difficult, in view of all the facts both past and present, to imagine how the conditions necessary for the age and area relation can ever have prevailed to any appreciable extent.

As to the hollow curves, their explanation is still not completely clear. Mathematically the "hollow curve" is part of what is called a Poisson curve, that is to say a frequency curve shifted to one side. More mathematically still it may be described as a frequency curve in which the variate (in this case the number of species per genus) is discrete and limited in one direction (here it never has a value less than one). Why it should appear in such biological connections as plant distribution is not so clear, and this is perhaps the main stumbling block regarding it. If one who is in no sense a mathematician may be allowed to express an opinion it is that curves of this kind may really be expressions of the methods used in biological classification, and not of anything vital in the organisms

concerned. In short, it may be suggested that they express more than anything else the accidents of human diagnosis.

Despite the considerable criticism that the detailed theory of Age and Area has received (18, 90, 210, 221) it must always be remembered that Willis rendered the cause of plant geography an enormous service by publishing it. As a result the subject of plant distribution quickly became topical and gained once more the attention it had previously largely lost, and to Willis must be credited much of the reputation that it now enjoys. It served also to focus study on just those aspects of the subject where it was most needed in view of other modern theories.

Differentiation

The Theory of Differentiation, just mentioned, is, as far as plant geography goes, especially associated with the names of Guppy (106, 108, 110) and Willis (291).

As Guppy inferred, the conception behind differentiation is not easily expressed in words, but it has been called the antithesis of the Darwinian Theory of Natural Selection by which there is imagined a gradual accumulation of morphological differences in the course of evolution, and according to which new species, genera and families appear chronologically in the order named. The differentiation view, on the contrary, is that generalised plant types, such as many families, tend to appear first in time, and only subsequently to differentiate into numerous genera and more numerous species. In Guppy's own words, "Differentiation is the view that the history of our globe, as far as secondary causes are in operation, is essentially the history of the differentiation of primitive world-ranging generalised types in response to the differentiation of their conditions."

As the present writer sees it this difference in outlook is but another aspect of the problem of small and large changes in evolution. On the former view it is difficult to imagine the sudden appearance of a markedly distinctive form such as might characterise a family, while on the latter there is no reason why this should not happen. At the same time it seems clear that the differentiation hypothesis only begs the real question because, even if later rather than sooner, the production of numerous closely related species or genera can only occur through the agencies of changes of comparatively small dimensions. These changes must in fact be capable of producing the kinds of differences which are commonly made the basis of specific and generic classification.

With that expression of opinion we must leave the critical consideration of differentiation, and the reader may be referred to Willis' recent treatment of the subject (291), but it is important to consider some of the ways in which Guppy suggests it affects the subject of plant geography.

He was much impressed by the fact that the families of Flowering Plants fall into two classes on a combination of geographical and structural characters. They are either wide-ranging primitive families or restricted derived families. He also emphasises that, as regards the larger groups and especially the families again, the principle that community between the Old and New Worlds is an affair of the north is not true. He mentions particularly the families of the warmer zones which are for the most part pan-tropical and which show little association with the geographical distinction between the two hemispheres.

This he associates in an interesting way with the known course of climatic and plant history, and particularly with the view that the earlier history of the

development of the Flowering Plants was one of widespread genial and more or less constant climate, while their later story has been linked with great climatic diversity and austerity. The same belief is arrived at on various grounds in the course of this book and is discussed at length in the final chapter, but the reason for mentioning it here in connection with differentiation is that Guppy associates it definitely with problems of species formation, and in doing so makes a noteworthy contribution to what we have called the evolutionary background.

He (106) "postulates for terrestrial plants an era when uniformity in environment was the rule—an era, one might imagine, of great atmospheric humidity, when persistent cloud-coverings blanketed the globe and when the same equable temperature everywhere prevailed," and he "pictures a plant-organism under such conditions as behaving very much like a ship in a calm, drifting in a morphological sense in all directions and displaying unchecked and irresponsible variation of the floral organs. . . ." Again, he says "this would imply that the mutations of the floral organs of our own day represent all that remains of the capacity of great morphological changes in the early days of the history of the Angiosperms."

In short he expresses the view that changes in environmental conditions may be reflected in plants in the manner in which their evolution proceeds, so that while in one set of conditions one method of evolution may predominate another may prevail when the conditions become markedly different. He infers indeed that the past may well have seen certain periods and conditions in which species production was especially copious. It has already been shown that there is some experimental reason for supposing this to have been the case, but it is of special interest to see this very important conception put forward in the particularly vivid way quoted.

CHAPTER 4

THE DISTRIBUTION OF FAMILIES

The Number and Size of Families

ESTIMATES of the number of families into which the Flowering Plants should be divided vary greatly. Bentham and Hooker (13), whose system is most familiar to British botanists, recognised about 200, but the most recent edition of Engler's system (71) includes about 280 and in some other modern classifications the number is even higher.

There is, in fact, a general tendency for the number to increase with the passage of time, not only because new families continue to be discovered, but because it becomes ever more apparent that the earlier conceptions of many of them were too wide and must be revised in the light of modern knowledge. Even to-day the process has not been carried as far as it might and there is little doubt that the number of families is still too small to give a true picture of their relationships.

For these reasons it is desirable to take as a basis for consideration a classification which goes as far as can at present be expected in this direction, and such is available readily in the system proposed by Hutchinson (136). He divides the Angiosperms into 332 families and thereby makes clear a number of important points which would otherwise be obscure, and except in certain minor directions which can be dealt with as they arise, his classification is followed in this and succeeding chapters.

Families vary greatly also in size, that is to say in the number of genera and species they contain. Some comprise only a single species each and are therefore of minimum size, but at the other extreme is one family at least containing over 1,000 genera and perhaps 20,000 species. This is the Compositae, which on any estimate must be considered the largest of all families, but the Orchidaceae and the Gramineae, both Monocotyledonous families, have several hundred genera and many thousands of species. Between these extremes there are other families of almost every size, and some of the figures relating to them are given below.

Widely Distributed Families

In discussing the geography of families it is obviously convenient to arrange them according to their ranges, and this course is adopted in the following pages, where the different types are discussed one after the other, beginning with those most widely spread and ending with the most restricted.

The first question that arises is whether there are any cosmopolitan families, by which is meant families which occur in all parts of the world. In so far as the polar regions are devoid of flowering plants there can of course be none, but in matters of plant geography the term cosmopolitan is usually taken to mean a distribution which comprises all those parts of the world where these plants can exist, and on this basis there are numerous cosmopolitan families.



FIG. 2.—A. *Stylidium scandens*, B. *S. tenellum*, and C. *S. pycnanthum*, about natural size, after Mildbraed.

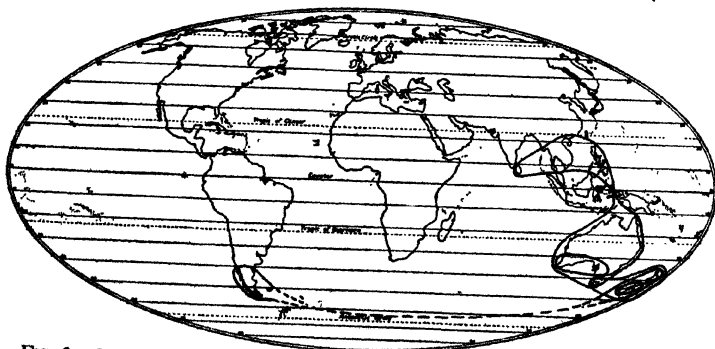


FIG. 3.—Map showing the distribution of the genera of the family Stylidiaceae.

On the score of absolute completeness of distribution the Gramineae (which include the bamboos, Plate 22) stand out pre-eminently. Not only are members of this family found over the widest extremes of latitude and longitude but their degree of distribution within this total outline is particularly dense and continuous. Almost alone among flowering plants grasses form the dominant element in the vegetation over great areas of the world, and nearly everywhere else too the proportion of these plants in the vegetation is very high.

The Compositae most nearly approach the condition shown by the Gramineae and in extent of range this family is probably almost as widespread, but its species, though much more numerous, do not often form so dominant a part of the vegetation. Nevertheless the genera are well scattered and nearly every flora contains a good proportion of them. In places they are especially abundant though there is no very outstanding local massing.

The families Papilionaceae, Scrophulariaceae, Liliaceae and perhaps the Amaryllidaceae are most nearly comparable with the grasses and Composites in range, all having the same generalised distribution without any very marked massing.

The other families which can claim a cosmopolitan or subcosmopolitan range fall into three fairly well-marked groups. The first of these comprises families which are predominantly either tropical or temperate but which have some representation in the remaining parts of the world. The second comprises families in which most of the genera are comparatively localised but which include also one or very few genera of exceptionally wide range. The third contains families whose members are mostly very widespread freshwater aquatic plants.

The first includes the three very large families Rubiaceae, Euphorbiaceae and Orchidaceae. These are found all over the world, but the great bulk of their species inhabit the tropics, their temperate members being for the most part specialised and rather unusual forms. The first-named, for instance, consists mainly of tropical shrubs and trees, and the bedstraws, which represent the family in the temperate regions, are very different-looking plants. The Euphorbiaceae, again, were it not for the very widespread genus *Euphorbia* and one or two others, would be almost exclusively a tropical family, while the small terrestrial orchids of the temperate zones are insignificant compared with the striking tropical members of the family.

Other but less notable families showing the same state of affairs are the Amaranthaceae, Cucurbitaceae, Loranthaceae, Malvaceae and Verbenaceae, the last named being particularly poorly developed in the Old World temperate regions.

The converse of these families is seen especially in the Ranunculaceae, Labiatae, Umbelliferae, Cruciferae, Caryophyllaceae, Campanulaceae and Rosaceae, all of which are markedly temperate groups, their wide actual ranges being due to the occurrence of a few forms in the tropics. In the Umbelliferae more especially, these latter are mostly confined to mountainous regions.

The other families with this kind of distribution are fourteen in number, namely :

Celastraceae, Chenopodiaceae, Gentianaceae, Hypericaceae, Iridaceae, Lythraceae, Oleaceae, Primulaceae, Rhamnaceae, Thymelaeaceae, Tiliaceae, Ulmaceae, Urticaceae and Violaceae.

These are on the whole smaller than those first mentioned and in most of them one or two genera are conspicuously larger and more widely spread than the rest,



FIG. 4.—*Drimys Winteri**, about natural size, after Baillon.

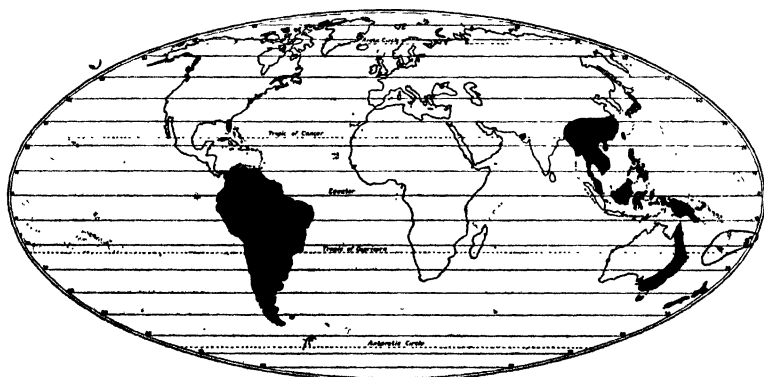


FIG. 5.—Map showing (black) the distribution of the family Winteraceae, including the discontinuous genera *Illicium* and *Drimys*, after Hutchinson.

* According to Smith, in *Journ. Arnold Arboretum*, 24, 1943, the plant depicted is the variety *punctata*.

but except for the *Chenopodiaceae* and *Primulaceae* they do not call for any further special comment in this brief general survey.

The *Chenopodiaceae* are remarkable in two respects. A great many of the species are halophytes, growing only where there is an appreciable amount of salt in the soil water. This condition prevails not only on sea coasts but also in many of the interior deserts of the world such as those of Australia and Asia, and here members of this family are sometimes almost the only plants present.

The *Chenopodiaceae* might therefore be expected to show a rather discontinuous distribution, but they are in fact almost cosmopolitan because of the very wide ranges of certain species of *Chenopodium*. These are, it is true, mostly plants of disturbed ground and are therefore often adventive, but their general effect is to make the family very widespread.

The families which owe their world-wide distribution chiefly to one particularly large and wide ranging genus number seventeen, among which the *Cyperaceae* and *Solanaceae* are most noteworthy. In the former the genus *Carex*, with upwards of 1,000 species, is one of the most cosmopolitan of all genera and in the latter the genus *Solanum*, with an even greater number of species, is found in all but the very coldest parts of the world. The other families are:

Aquifoliaceae, *Aristolochiaceae*, *Convolvulaceae*, *Eriocaulaceae*, *Geraniaceae*, *Juncaceae*, *Linaceae*, *Lobeliaceae*, *Onagraceae*, *Oxalidaceae*, *Papaveraceae*, *Plantaginaceae*, *Polygalaceae*, *Polygonaceae* and *Portulacaceae*.

The family *Plantaginaceae* is specially remarkable in that it virtually consists of one very large genus only.

There might perhaps be added to this group the families *Droseraceae*, *Lentibulariaceae*, *Orobanchaceae* and *Santalaceae*, which although scarcely cosmopolitan are all very widely distributed, and each of which consists mainly of one large genus. It is better, however, to mention them separately because their ranges are correlated with their peculiar physiological relations, the two former being insectivorous and the two latter parasitic.

The more or less aquatic families number about a dozen and are:

Alismataceae, *Butomaceae*, *Callitrichaceae*, *Ceratophyllaceae*, *Elatinaceae*, *Haloragaceae*, *Hydrocharitaceae*, *Juncaginaceae*, *Lemnaceae*, *Najadaceae*, *Nymphaeaceae*, *Potamogetonaceae* and *Zannichelliaceae*.

All contain a good proportion of floating or submerged plants and all are small, four containing one genus only. The exceptionally wide range of many aquatic plants, and especially such as are free-floating is a well-known feature of plant geography and will be discussed elsewhere, and these families must be remembered as containing most of the best instances of it.

There remain some nine families which are so widely distributed that they must be regarded at least as subcosmopolitan but which possess certain features which make it undesirable to force them into the foregoing rough classification.

The *Araceae* are very widespread but only as a result of a slight and rather specialised temperate representation. The family is really tropical and very few of the species are found outside that zone. It therefore resembles the *Euphorbiaceae*, but the temperate members are fewer and much less completely distributed.

The *Boraginaceae*, with about 100 genera, is much the same size as the *Araceae*, but here the difficulty is rather different. The family as usually delimited is predominantly temperate and the temperate members are all or almost all herbs of characteristic appearance. The tropical representatives, in virtue of which

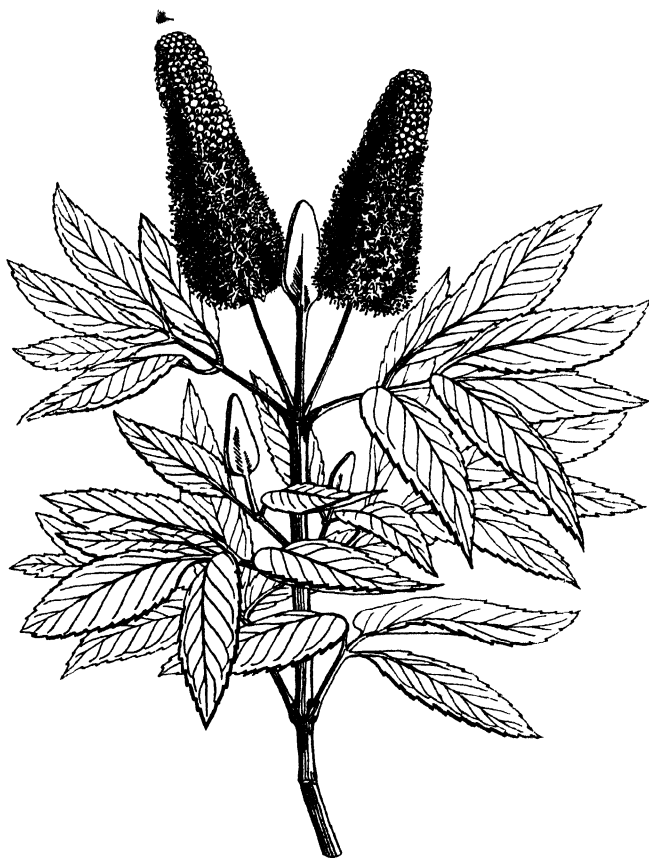


FIG. 6—*Cunonia capensis*, about half natural size, after Baillon

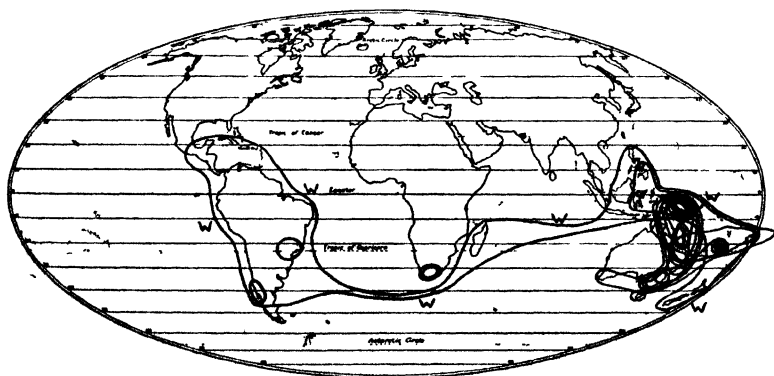


FIG. 7.—Map showing the distribution of the genera of the family Cunoniaceae. One genus, *Weinmannia*, represented by the letter W, is very widespread; all the rest are more or less narrowly endemic and much concentrated in New Guinea and Australasia.

the family is cosmopolitan, are fewer and mostly shrubs or trees, superficially at least quite unlike the typical temperate members of the family. It is impossible to avoid the suspicion that the family thus constituted does in fact include more than one natural group. If this is so, then any description of its distribution must be regarded with caution.

This point is seen even more plainly in the Ericaceae. As delimited by Hutchinson (136) (and his procedure is quite as conservative as that of many others) the family is world-wide, but the details of its constitution and those of the ranges of its different subfamilies are such as to make it hard to believe that the Ericaceae are on this definition, a natural group.

For instance it comprises four subfamilies, two of which are rather similar and the others markedly different. The two most important of these are exemplified by the genera *Rhododendron* and *Erica* respectively and the differences, both structural and geographic, between these two genera alone are enough to cause misgivings. The family seems to need revision, and if and when this is done its range will almost certainly not be so wide.

The Crassulaceae are anomalous because their wide distribution is due to one or two small and almost ubiquitous subaquatic genera very unlike most members of the family, which are strongly marked xerophytes. This larger part of the family is notably massed in South Africa and in the Mediterranean and Macaronesian regions.

Then there are one or two families, which although widespread, show conspicuous gaps in their ranges. Such are the Illecebraceae, notably absent from Asia, the Typhaceae, apparently not found in South America, and the Caprifoliaceae, practically absent from Africa.

The Zygophyllaceae resemble the Chenopodiaceae in the number of halophytes and the family also has many xerophytes, but it lacks the widespread forms like *Chenopodium*, and thus its range although totally wide is much less complete.

Much the same is true of the Plumbaginaceae except that this family is rather more particularly maritime. It is thus extensive at least in one direction but rather restricted in another sense.

Tropical Families

Next to the cosmopolitan and very wide families there come, in point of wideness of distribution, the numerous families which have a more or less pan-tropical range. Since the tropical regions comprise three widely separated areas these families are in a sense discontinuous, but, as was explained earlier, the fact that they occupy the whole of the land surfaces of a major climatic zone may be taken to override this and makes it convenient to consider them as constituting a separate category.

These families number eighty in all, and most of them are truly pan-tropical, although a few are absent from one or two minor areas. Most of them, too, are more or less evenly spread over the whole region, but some are predominant in one or other of the three parts. It would occupy too much space here to go into these details and the families must be considered all together, but they can be split into several groups according to their size and to the proportion of genera and species in them.

Seventeen families are considerably larger than the rest, having many genera

and not much less than 1,000 species each, and in some considerably more. Roughly in diminishing order of size these are :

Myrtaceae, Melastomataceae, Acanthaceae, Asclepiadaceae, Mimosaceae, Palmae, Gesneriaceae, Apocynaceae, Sapindaceae, Lauraceae, Myrsinaceae, Caesalpiniaceae, Guttiferae, Rutaceae, Moraceae, Annonaceae and Zingiberaceae.

Families of second size, with numerous genera and several hundreds of species each are (alphabetically) :

Agavaceae, Anacardiaceae, Araliaceae, Bignoniaceae, Capparidaceae, Comelinaceae, Flacourtiaceae, Icacinaceae, Loganiaceae, Malpighiaceae, Meliaceae, Menispermaceae, Monimiaceae, Samydaceae, Sapotaceae and Sterculiaceae.

Smaller again, and with not more than about 25 genera each, are :

Bombacaceae, Burseraceae, Combretaceae, Connaraceae, Dilleniaceae, Hydrophyllaceae, Lecythidaceae, Marantaceae, Myristicaceae, Nyctaginaceae, Ochnaceae, Olacaceae, Passifloraceae, Podostemaceae, Simaroubaceae and Theaceae.

The Escalloniaceae may perhaps also be mentioned here, although they have also a strong temperate representation in the southern hemisphere.

On the score of species numbers about a dozen other families must be reckoned as large or very large, but these all have but few genera and their wideness of range is generally due to the exceptional distribution of one or very few of these. The Piperaceae, with only 7 genera but over 1,000 species, and the Begoniaceae, with 4 and 700, are the most outstanding of this type, but the following also show the same feature to varying extents :

Aizoaceae, Chailletiaceae, Dioscoreaceae, Ebenaceae, Erythroxylaceae, Hippocrateaceae, Hypoxidaceae, Smilacaceae, Turneraceae, and Vitaceae.

All the rest of the tropical families are very much smaller than any already mentioned. Four of them, namely Balanophoraceae, Pedaliaceae, Phytolaccaceae, and Rhizophoraceae, and generally reckoned to have more than 10 genera, but the remainder are even smaller. They all must be regarded, however, as at least sub-pan-tropical in range and comprise :

Basellaceae, Bixaceae, Burmanniaceae, Buxaceae, Cannaceae, Cochlospermaceae, Cytinaceae, Hernandiaceae, Molluginaceae, Opiliaceae, Pontederiaceae, Taccaceae, Thismiaceae, Triuridaceae and Xyridaceae.

Temperate Families

Having recognised a tropical category, it is only appropriate to attempt to bring together families which show the opposite type of range, that is to say which are confined to the temperate zones of the world. It is, however, not easy to do so because the north and south temperate regions are widely separated and there are few families found in both which are not also found in the more elevated parts of the intervening parts of the tropics and which thus have an almost world-wide range. Indeed many of the families which have already been described as cosmopolitan are more properly described as temperate families since they do not occur in the lowlands of the tropics. Despite this difficulty there are, however, certain families which are practically confined to the extra-tropical parts of the world or to a large part of them and which are best considered here as a separate group.

These number about twenty, and seven of them are found only in the northern temperate zone, namely :



FIG 10 —*Hypolaena fastigiata*, a typical member of the Restionaceae, about natural size, after Hooker

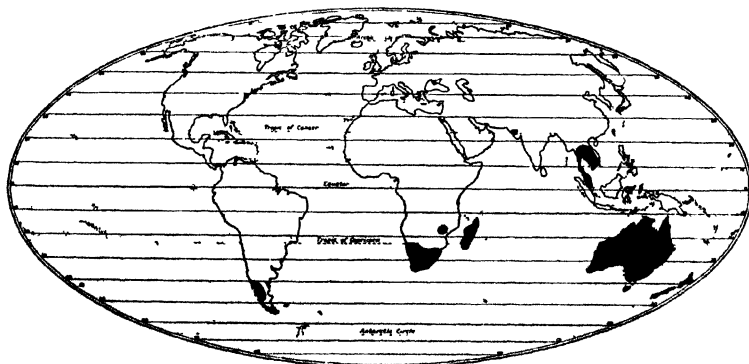


FIG 11 —Map showing (black) the distribution of the family Restionaceae, partly after Hutchinson

Adoxaceae, Cannabinaceae, Corylaceae, Diapensiaceae, Monotropaceae, Scheuchzeriaceae and Trilliaceae.

They are all small families, the largest, Corylaceae, having only 4 genera and less than 50 species, and the Adoxaceae and Scheuchzeriaceae only 1 species each. The Diapensiaceae are remarkable in being almost entirely arctic-alpine.

Most of the remaining dozen or so families are widely distributed in the northern temperate zone but have in addition some extension into and across the tropics in one or other direction. Most conspicuous, perhaps, of these are the Berberidaceae, Grossulariaceae and Polemoniaceae, which are not only circumboreal but extend south throughout America along the Andes. In the first two the extension is due to the genera *Berberis* and *Ribes* respectively, but the Polemoniaceae are really an American family and circumpolar only by one well-known species, *Polemonium caeruleum*.

The Salicaceae and Saxifragaceae resemble the above, but extend fairly completely also through Africa; while in the three families Aceraceae, Elaeagnaceae and Juglandaceae the extension (most marked in the first-named) is south and east into tropical Asia.

The Hamamelidaceae are somewhat discontinuous, but a recent revision (73) gives them a fairly complete northern range with some extension into both Africa and tropical Asia.

The Resedaceae are the only family with a southern extension confined to Africa and this is correlated with the fact that the family is centred in the Mediterranean region, the rest of its northern representation being but slight.

The small aquatic family Ruppiaceae is generally described as pan-temperate and is indeed almost confined to the temperate zones, its occurrence in the tropics being scanty.

Finally, the family Zosteraceae, which contains two of the few genera of marine Angiosperms, is within its ecological limitations more or less pan-temperate since it is found on nearly all coasts outside the tropics.

In concluding this short survey of tropical and temperate families it is appropriate to refer to the fact that a family of the one kind is often complementary to a family of the other and that a tropical family may be the counterpart of a temperate family or *vice versa*. The Campanulaceae and Lobeliaceae provide an instance of this, the former being mainly temperate and the latter tropical. Another well-marked instance is afforded by the Umbelliferae and the Araliaceae which are similarly distributed. In both cases the structural relation between the two families is very close.

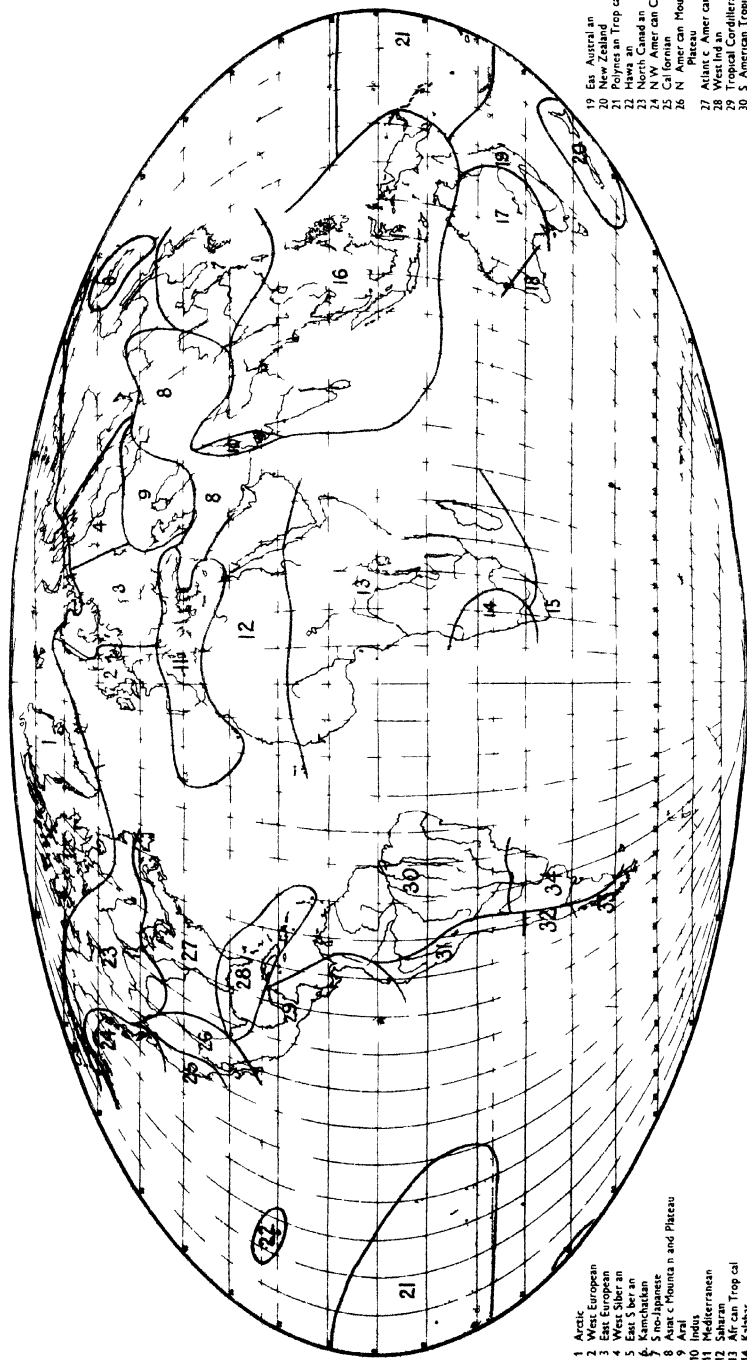
Discontinuous Families

In the categories just considered the distribution of the families includes the whole of one or both of the major climatic zones of the world, the tropical and temperate, and there have now to be described the families whose ranges are less than the whole of one of these zones. There are two types of such families, first the discontinuous, in which the total range may be great but in which the actual areas occupied comprise two or more distinct and separate areas, and the endemic, in which the total range is more or less markedly restricted.

The discontinuous families are best divided into groups, recalling and using

Map of the World showing Climatic Provinces After
 Supan in Bartholomew's Physical Atlas vol III

PLATE 5



- 1 Arctic
- 2 West European
- 3 East European
- 4 West Siberian
- 5 East Siberian
- 6 Frost-belt
- 7 Frost-belt
- 8 Asia's Mountain and Plateau
- 9 Arid
- 10 India
- 11 West African
- 12 Saharan
- 13 African Tropical
- 14 Kalbar
- 15 Cape Australian Monsoon
- 16 East Australian
- 17 Inner Australian
- 18 S.W. Australian
- 19 East Australian
- 20 New Zealand
- 21 Polynesian Tropical
- 22 Hawaii
- 23 Hawaiian
- 24 N.W. American Coastal
- 25 Californian
- 26 N. American Mountain
- 27 Atlantic American
- 28 West Indian
- 29 Tropical Cordilleran
- 30 S. American Tropical
- 31 North Chilean
- 32 South Chilean
- 33 Pampas

Areas correct to 1000 000 000 1600 m. each a g. g. a. o.
 Approximate Scale 1:100 000 000 1600 m. each a g. g. a. o.
 on Mollweide's Homolographic Projection

for the purpose the two main geographical facts that the two temperate zones are separated by the intervening tropics and that there are three great and separate land masses extending south from the continuous circumboreal belt. Many discontinuities are the result of the restriction of families either to the two widely separate temperate zones or to two or all of the three southern extensions. Apart from these, discontinuity is usually the result of incomplete distribution within one of these major areas.

It is convenient to record the discontinuous families in tabular form because this presents the very varied facts most easily and also indicates the relative prevalence of each type. The table given is, of course, capable of much further subdivision, but it is unnecessary to go into any very great detail here because in many cases the discontinuity is due to the distribution of particular genera and these will receive further attention later on.

The Discontinuous Families of Angiosperms

A. Families of the north and south temperate regions :

Betulaceae	.	north temperate and South America
Empetraceae (fig. 38)	.	north temperate, South America and Tristan da Cunha
Fumariaceae	.	north temperate (especially Mediterranean) and South Africa
Sparganiaceae	.	north temperate, Australia and New Zealand

B. Families of America and of Asia and/or Australasia :

1. Found predominantly or entirely in the northern hemisphere—

Calycanthaceae	Nyssaceae	Schisandraceae
Datiscaceae	Saururaceae	Styracaceae
Magnoliaceae		

2. Found predominantly in the tropics—

Cabombaceae	Roxburghiaceae	Sauraujaceae
Chloranthaceae	Sabiaceae	Symplocaceae

3. Found predominantly or entirely in the southern hemisphere—

Centrolepidaceae	Epacridaceae	Stylidiaceae (figs. 2, 3)
Corsiaceae	Eucryphiaceae	Winteraceae (figs. 4, 5)

4. Found in both hemispheres—

Lardizabalaceae

C. Families of America and Europe-Africa, sometimes in Madagascar, etc. :

1. Found in America and tropical Africa—

Bromeliaceae ? (Plates 7, 10)	Hydnoraceae	Strelitziaceae
Canellaceae	Loasaceae	Velloziaceae
Caricaceae	Mayacaceae	Vochysiaceae
Humiriaceae	Rapateaceae	

2. Found in America and the Mediterranean region—

Cistaceae

3. Found in South America and southern Africa—

Tecophilaeaceae

D. Families of Africa (and/or Madagascar, etc.) and of Asia and/or Australasia :

Alangiaceae	Dipterocarpaceae	Pandanaceae
Ancistrocladaceae	Flagellariaceae	Pittosporaceae
Aponogetonaceae	Musaceae	Sonneratiaceae
Casuarinaceae	Nepenthaceae	Trichopodaceae

E. Families discontinuously distributed in the northern temperate zone :

Cynocrambaceae	Platanaceae
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F. Families found in all three parts of the southern hemisphere :

Cunoniaceae (figs. 6, 7)	Philesiaceae (figs. 8, 9)	Restionaceae (figs.10,11)
Haemodoridae	Proteaceae (figs. 14, 15)	

G. Other discontinuous families :

Clethraceae .	only genus <i>Clethra</i> (figs. 31, 32)
Coriariaceae .	only genus <i>Coriaria</i> (figs. 36, 37)
Cornaceae .	north temperate, Africa, Madagascar, east Asia, temperate South America, New Zealand
Fagaceae .	north temperate, all Asia, Australasia, temperate South America
Frankeniaceae .	Europe to India and South Africa, western North America, temperate South America, Australia
Hydrangeaceae .	north temperate, tropical America, tropical Asia, and Hawaii
Oliniaceae .	St. Helena, South and East Africa
Phylodraceae .	Asia and Australia
Posidoniaceae .	a marine family, see Plate 15
Stackhousiaceae .	Philippines, Australia and New Zealand
Staphyleaceae .	Parts of north temperate and tropical America and Asia

Three families which might be sought in the above lists are excluded. They are :

Batidaceae .	Best treated as endemic to America as it is probably adventive in Hawaii. It may be somewhat discontinuous in America.
Byblidaceae .	The most recent study of this group splits it into two separate families, Byblidaceae and Roridulaceae.
Myoporaceae .	Very doubtfully a natural group.

Endemic Families

As was explained in a former chapter the term "endemic" is not an absolute one but varies according to the circumstances in which it is employed, and it is therefore necessary to determine how the term shall be used here and what shall be included in it. As regards species it is generally used in a very narrow geographical sense, and with genera also it is usually comparatively restricted, but with families, which rank among the larger of classificatory units, its employment must be on a wider basis. The only real criterion is one of practical convenience and the word is best used here to mean families which are found either within one of the continental land masses or in some area of equivalent size. Many families are more restricted even than this, but to make the category less wide would involve excluding some which must on all counts be included.

The endemic families are here tabulated on a geographical arrangement and are accompanied by figures indicating the *approximate* number of species in each, since this is a matter of special interest in endemic groups.

The Endemic Families of Angiosperms

A. America :

1. North	Crossosomataceae	3
	Garryaceae	20
	Leitneriaceae	2
	Lennoaceae	5
	Limnanthaceae	5
2. Tropics	Alstroemeriaceae	175
	Batidaceae	1
	Brunelliaceae	10
	Cactaceae	2,000 (Plates 6, 10)
	Caryocaraceae	20
	Columelliaceae	3
	Cyclanthaceae	50
	Cyrtillaceae	6
	Diclidanthaceae	3
	Fouquieriaceae	5
	Julianiaceae	5
	Laciniaceae	20
	Lissocarpaceae	1
	Malesherbiaceae	25
	Marcgraviaceae	50
	Quiinaceae	25
	Thurniaceae	2 British Guiana
	Tovariaceae	2
	Trigoniaceae	30
	Tropaeolaceae	30 (fig. 12)

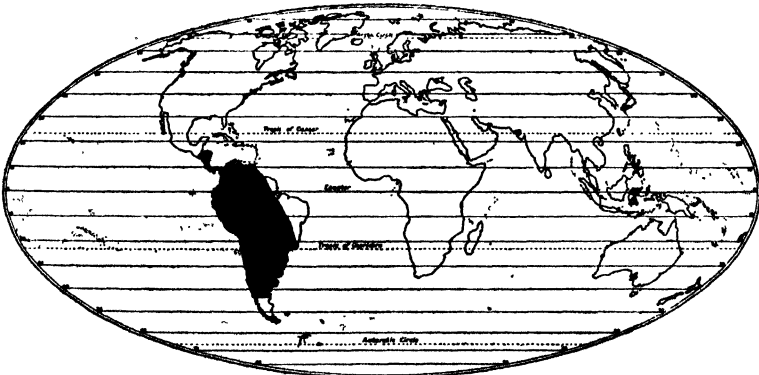


FIG. 12.—Map showing (black) the distribution of the family Tropaeolaceae, after Hutchinson.

3. Southern	Gomortegaceae	1	
	Lactoridaceae	1	Juan Fernandez
	Myzodendraceae	12	
4. Others	Calyceaceae	30	Tropical and South
	Heterostylaceae	1	Andes
	Sarraceniaceae	10	North and Tropical

B. Mediterranean in a wide sense :

Cneoraceae	15
Globulariaceae	25
Ruscaceae	150

C. Africa :

1. Africa tropical or south, and Madagascar, etc.

Hydrostachyaceae	12
Selaginaceae	250

2. Tropical Africa

Barbeyaceae	1	
Heteropyxidaceae	2	
Melanthaceae	20	
Myrothamnaceae	1	and Madagascar
Octoknemataceae	5	
Pandaceae	1	
Scyttopetalaceae	12	

3. Madagascar or Mascarenes only

Chlaenaceae	30
Didiereaceae	4
Medusagynaceae	1 Seychelles

4. Southern Africa

Achariaceae	3
Bruniaceae	30
Geissolomataceae	1
Greyiaceae	3
Grubbiaceae	3
Penaecaceae	30
Roridulaceae	2

D. Asia :

1. Continental and extra-Malayan

Actinidiaceae	12
Cercidiphyllaceae	2
Circaeasteraceae	1
Eucommiaceae	1
Punicaceae	2
Sargentodoxaceae	1
Stachyuraceae	5
Trochodendraceae	6

2. Others

Crypttroniaceae	8
Gonystylaceae	7
Lowiaceae	2
Petrosaviaceae	3
Scyphostegiaceae	1
Stenomeridaceae	3

E. Australasia and the Pacific Islands :

1. Australia only	Akaniaceae	1	
	Byblidaceae	2	
	Cephalotaceae	1	south-west Australia
	Petermanniaceae	1	
	Tremandraceae	30	
2. Others	Balanopsidaceae	7	New Caledonia
	Corynocarpaceae	3	New Zealand, New Caledonia, New Hebrides
	Eupomatiaceae	2	Australia and New Guinea
	Himantandraceae	3	Australia and New Guinea
	Xanthorrhoeaceae	12	Australia and New Caledonia

The actual ranges of these endemic families naturally vary greatly, if for no other reason than that they are very different in size, and as might be expected the most narrow are among the monotypic families. Perhaps the most local of all are the Cephalotaceae found only in the neighbourhood of King George's Sound in Western Australia, the Lactoridaceae on Juan Fernandez, and the Medusagynaceae on the Seychelles.

The absence of the Bromeliaceae and their inclusion earlier in the discontinuous families requires explanation. This family has long been regarded as an American endemic family, and with its 1,200 species as the second largest of all endemic families (232). Recently, however, a member of the genus *Pitcairnia* has been collected in western tropical Africa and described as new. This record cannot yet be accepted unconditionally, and there is always the chance that the plant may in fact be adventive, as is apparently the case with the Old World forms of the Cactaceae. In the circumstances the family is included in the discontinuous families with a query.

Anomalous Families

There remain to be mentioned certain families which do not fit easily into the classification just given, and as each has points of special interest they are worth separate notice.

Several families of wide distribution cannot fairly be called either tropical or temperate. The Balsaminaceae, for instance, while found throughout the northern temperate zone are most strongly developed in tropical Africa and tropical Asia. The same is true of the Vacciniaceae, but here the tropical representation is specially strong in America and Asia. There are also species in America and in Fiji. Most conceptions of the Myricaceae, too, give that family a somewhat similar type of range, except that the tropical development is wider though less marked.

In lesser degree the Valerianaceae are the same. The family is specially well represented in the north temperate, but it has so many species in warmer regions that it cannot be labelled as a purely temperate group.

Several families are as narrow as many endemics but actually cover parts of two continents. The Moringaceae, Salvadoraceae and Tamaricaceae are all small and chiefly desert families of North Africa and western and central Asia. The Dipsacaceae range from Europe to India. The Apostasiaceae are also a small group fairly widespread in tropical Asia and reaching Australia.

Lastly, in the Goodeniaceae the exceptional distribution of two sea-dispersed

strand plants of the genus *Scaevola* makes the family as a whole almost pan-tropical, but to describe it so obscures its two main features, which are the massing of nearly all its species in south-west Australia and the occurrence of one genus in New Zealand and temperate South America.

Southern Families

No one arrangement of the families can be made to emphasise all the points of interest they present when compared, and although the foregoing is probably the most useful on general grounds, there is one matter not very apparent in it but of such theoretical importance that it calls for special treatment. This is the relative distribution of the families in the northern and southern hemispheres respectively, or more shortly the question of whether there are any really southern families, that is to say families specially characteristic of the southern hemisphere, and if so how many.

Of the three-hundred-odd families recognised by Hutchinson just under fifty are actually entirely or predominantly confined to the lands south of the equator, this predominance including both extent of range and balance of numbers. Of these fifty or so, about eighteen are endemic and have already been noted.

Of the thirty remaining families a group of nine may be described as wide southern in the sense that they are found well distributed over more or less the whole southern hemisphere. They are:

Cunoniaceae (figs. 6, 7), Escalloniaceae, Haemodoridae, Haloragaceae, Hypoxidaceae, Monimiaceae, Myoporaceae, Myrtaceae and Philesiaceae (figs. 8, 9).

But the Haloragaceae are rather anomalous because the southern predominance is due to one genus only, *Gunnera* (fig. 44), while the Myoporaceae are an unsatisfactory group.

Several of these families extend across the equator northwards to some degree, and this is specially true of the Myrtaceae, though the great bulk of its species are either South American or Australian.

Five more families may also be called wide southern, but with the difference that they are markedly centred families and much of their total range is due to comparatively few forms. The *Aizoaceae*, for instance, have an enormous concentration in South Africa because of the great development there of the polymorphic genus *Mesembryanthemum*, but a few of its members have a much wider range. Similarly, the family Oxalidaceae, which in total is almost cosmopolitan, has the vast majority of its species in South Africa or South America, in both of which the genus *Oxalis* is greatly developed. The Thymelaeaceae again have their greatest concentration in South Africa and Australasia, but the southern predominance is perhaps less than in the others. In addition the Proteaceae and Restionaceae, which are among the best-known of all southern families, while occurring all over the south and slightly in the north too, are very predominantly South African and Australian.

Another conspicuous group of southern families consists of those which are practically confined to Australia and/or New Zealand, but have various minor extensions therefrom, sometimes for considerable distances, namely:

Casuarinaceae, Centrolepidaceae, Corynocarpaceae, Epacridaceae, Goodeniaceae, Himantandraceae, Phylodraceae, Pittosporaceae, Stackhousiaceae, Stylidiaceae and Xanthorrhoeaceae.

The Pittosporaceae are entirely confined to Australia except for the large genus *Pittosporum*, which is found all over the Old World tropics, this being the most considerable extension shown by any of the eleven families, certain features of the Casuarinaceae and Goodeniaceae not being quite comparable. The Centrolepidaceae, Epacridaceae, Goodeniaceae and Stylidiaceae extend both into tropical Asia and to temperate South America, the second and third also reaching the Pacific Islands. The Goodeniaceae, however, are complicated by the two strand plants already mentioned.

The Casuarinaceae, Corynocarpaceae and Xanthorrhoeaceae also extend to both Asia and Polynesia, but scarcely comparably. In the last named the extension is only to New Guinea and New Caledonia, while the second family does not occur in Australia but only in New Zealand. The first is complicated by a single widespread strand plant.

The Himantandraceae, Phylodraceae and Stackhousiaceae extend only to Asia, the first only to New Guinea and the second to China.

Finally, there are three small families which are widely discontinuous, namely the Corsiaceae (Chile and New Guinea), Canellaceae (America and Australasia), and Eucryphiaceae (Chile and Australia). The distributions of the first two are of doubtful significance as the families are rather problematical.

Details of some Particular Families

The total range of a family is simply the sum of the ranges of its constituent genera and species and, except in very small families, reveals little about the relative and proportionate distribution of these minor units, which is actually often the most noteworthy feature in their distribution as a whole. Moreover, this varies greatly, with the result that families whose total ranges are very similar are often very distinct in terms of the distribution of their genera. Indeed, it would be quite possible to arrange all the families actually on this basis, but this would occupy too much space here. As a substitute, the remainder of this chapter is devoted to a review of four particular families which, taken together, illustrate most of the salient features that a classification of this kind would show. These families are the Primulaceae, Palmae, Proteaceae and Lobeliaceae.

The Primulaceae

The Primulaceae may be described as an outstanding example of a family made up of a few, and comparatively widely different, genera which vary considerably in distributional extent. Its total range is practically world-wide, but most of the genera are much more restricted. The classification used here is that of Pax (69), with the figures as far as possible brought up to date.

There are 17 genera, namely, *Primula*, *Androsace*, *Soldanella*, *Pomatosace*, *Bryocarpum*, *Dodecatheon*, *Cyclamen*, *Lysimachia*, *Trientalis*, *Asterolinon*, *Pelletiera*, *Glaux*, *Anagallis*, *Centunculus*, *Samolus*, *Hottonia* and *Coris*. Most of them are temperate genera and generally familiar, so that a glance at the list shows how varied an assortment of types may go to make up a family which is nevertheless a well-defined natural group.

The world-wide distribution of the family is due chiefly to the exceptionally wide areas of *Anagallis* and *Samolus*. *Anagallis* especially is a genus of disturbed

ground and much of its range may be adventive, but *Samolus* appears to be truly and naturally almost cosmopolitan.

Primula is by far the largest genus, with several hundreds of species. Geographically it is both discontinuous and locally centred. It ranges throughout the northern temperate regions and has also one species at least in temperate South America, but the vast majority of its forms are confined to the great Sino-Himalayan mountain region. This latter region has been carefully explored only in recent years, and the discovery and frequently the subsequent introduction into European gardens of many new *Primula* species has been a marked feature in the horticultural history of this century. The genus *Androsace*, though smaller than *Primula*, rather closely resembles it, but is confined to the northern temperate zone.

Lysimachia is also a large genus and is found in almost all the temperate and subtropical parts of the world, as well as on some tropical mountains.

The remaining genera are all small in species number and also in range, and fall into several well-marked groups each of special interest. *Hottonia*, with 2 spp., is found in eastern North America and in Europe, and *Dodecatheon*, with about 15, occurs in North America and eastern Asia. *Bryocarpum* and *Pomatosace* are monotypic (of one species only) endemic genera of the Sino-Himalayan mountains. *Cyclamen*, 12 spp.; *Asterolinon*, 2 spp.; *Coris*, 2 spp.; and *Soldanella*, 7 spp., are all found only in Europe or the Mediterranean region, the last named being one of the few genera endemic to the European Alps. *Glaux*, 1 sp.; *Centunculus*, 3 spp.; and *Trientalis*, 2 spp., are fairly widespread in the northern temperate zone. Finally, *Pelletiera*, 2 spp., is found only in temperate South America; and *Samolus*, 12 spp., though almost cosmopolitan, has species in both north and south temperate zones.

The family thus illustrates the following points. It consists of comparatively few but markedly distinct genera. The genera vary in size from monotypes to one with hundreds of species. There is discontinuity both within the northern temperate zone and between the north and south temperate regions. It is in total world-wide but only by the exceptional ranges of one or two forms. Endemism is fairly well marked, and one genus, *Primula*, is an outstanding example of a group with the bulk of its species massed in one part of the world. The family is very predominantly temperate in character.

The Palmae

(Plate 25)

The family Palmae, containing that remarkable and almost unique group of plants known as the palms, differs from the Primulaceae in almost every way. It is a large group both in genera (about 180) and species (about 1,800) but it is at the same time a very natural one with a most distinctive appearance. Its geographical range, too, is very distinct (fig. 13), being rigidly limited by climatic conditions and almost entirely within the tropics. Indeed the Palmae are one of the most exclusively tropical of all families. Such climatic limitation is never absolute in a family of any size, and to this the Palmae are no exception, having a slight representation in several subtropical regions, but this only emphasises the tropical character of the family as a whole.

Within the tropics the distribution of the palms is ubiquitous, but by the nature

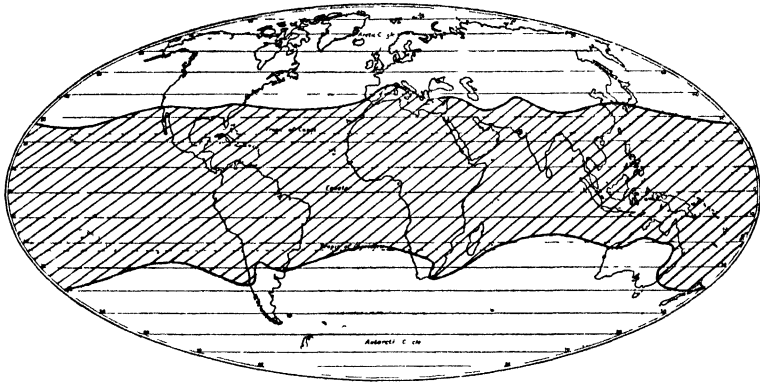


FIG. 13.—Map showing (shaded) the distribution of the family Palmae.

of the case it is divisible into three parts. About 60 of the genera are confined to the American continent: about 80 to Asia, Australia and the Pacific Islands; while only about 30 are restricted to Africa, including parts of the Mediterranean region. Only about seven genera range over more than one of these three areas and none is found in all three. *Phoenix*, *Borassus*, *Hyphaene* and *Calamus* are found in both Africa and Asia; *Raphia* and *Elaeis* in both America and Africa. *Pritchardia* is found in America and in the Hawaiian Islands. No genera occur in both America and Asia or Africa and the Pacific Islands.

The genera vary enormously in size. The largest is *Calamus*, with about 250 species, and *Geonoma* and *Bactris* have over 100 each. *Daemonorops*, *Pinanga*, *Licuala* and *Chamaedorea* are also large. On the other hand, no fewer than 65 genera are monotypic and at least 100 others are generally considered to have less than 5 species each.

The absence of wide genera has already been remarked, but in addition to this the number of genera with narrow ranges, namely endemics, is very large. Using the term endemic in quite a conservative sense, about 100 merit it and these are scattered almost all over the tropics and few regions are without them. They are least plentiful perhaps in Malaya and most abundant and conspicuous in certain small insular areas. Thus in the Seychelles and Mauritius as well as in South Africa, all the genera are endemic; in New Caledonia 14 out of 15 genera are endemic, and much the same is true of New Zealand. In Madagascar 10 out of 14 and about 90 per cent. of species are found nowhere else, and among other regions Central America has 8 endemic genera, the West Indies 3, New Guinea 6, and the Pacific Islands 5.

Species endemism is even more marked and it has been calculated that no less than 95 per cent. of all species in the family are so narrowly distributed. Not only this, but in nearly 150 genera there are nothing but endemic species. In Hawaii, South Africa, Madagascar and the Mascarenes, New Caledonia and New Zealand all the species are endemic, while even in such continental regions as Central America, South America, and tropical Africa the percentage is over 90. Similarly in New Guinea and the Pacific Islands; but in other parts of Malaya the proportion of endemic species (as also of endemic genera) is lower than

almost anywhere else, as for instance 50 per cent. in Java and 38 per cent. in Sumatra.

Even more noteworthy is the relationship between endemism and geographical isolation in the form of insularity, which is seen in both genera and species. Nearly 40 genera are restricted to what may reasonably be called small islands. There are, for instance, 14 endemic genera in New Caledonia and 9 among the smaller islands associated with Madagascar, including 6 on the Seychelles alone. There are also about 6 on various small islands of the Pacific as well as two on the tiny Lord Howe Islands near Australia, and one on Juan Fernandez.

This marked restriction of many palms to small islands is still better seen in the species, as the following table shows.

Species of Palms on Small Islands

Hawaiian Islands	16	Solomons	8
Bismarck Archipelago	12	Seychelles	8
Mauritius	11	Trinidad	7
Fiji	9		

4 species each on Martinique, Samoa, the Carolines, the Comoros, and St. Marie de Madagascar.

3 species each on the Andamans, the Nicobars, Aru, the Lord Howe Is., Ternate.

2 species each on Guadeloupe, Tuamotu Islands, Ceram, Nossi Bé, Tobago, Palau and St. Vincent.

Among the islands from which single endemic species have been recorded are : St. Thomas, Barbados, the Isle of Pines, Mergui, Bird Island, Bermuda, Aiguille, Fernando Po, Corisco, Key, Bougainville, Billiton, Christmas, Grenada, Croker Island, Batjan, Norfolk and St. Kitts.

The extraordinary degree of insularity exhibited by the palms is a matter of great interest and will be referred to again later, but at the moment it must suffice to mention two facts which doubtless contribute to the explanation of it. They are the considerable geological age of the family and, almost certainly more important, the fact that many palms have fruits which can undergo prolonged immersion and flotation in the sea without injury and which can germinate and establish themselves comparatively close to the water.

To summarise, the Palmae are a very natural group with a very isolated systematic position. The genera vary greatly in size, but an unusually large number of them are very small. The family is rigidly limited geographically to the warmest parts of the world's surface except for one or two quite minor extensions. No single species or even genus covers anything approaching the whole range of the family and widespread genera and species are very few. Such as there are show discontinuity over two of the three major land divisions of the tropics. Endemism in both genera and species is exceptionally high and is accompanied by an almost unique degree of geographical isolation, a number of species being confined to islands so small as to be difficult to find even in the largest atlases.

The Proteaceae

(Plates 12, 17, fig. 14)

This family is best known for the relationship it shows between southern Africa and Australia, but undue emphasis on this point has tended to obscure the main geographical feature of the group, namely that it is one of the best examples of a large southern family well represented in all the continents below the equator.

As will be seen from the map (fig. 15) there are three extensions northwards from the main areas of distribution, one in each continent. That in America is largely due to the genus *Roupala* which is well represented in Brazil and other parts of the neighbouring tropics, and in this continent the southern species are comparatively few. These show, however, a strong relation with Australia, both *Embothrium* and *Lomatia* (fig. 35) being discontinuous between the two continents.

The northern extension is least in Africa and is due entirely to the tropical distribution of members of characteristically South African genera such as *Leucospermum* and *Protea*, which range as far north as Abyssinia. There is a monotypic genus in Madagascar.

As in the New World the tropical extension of the family in Asia is due to one large genus, *Helicia*, which covers the whole of the monsoon region proper to the Bismarck Archipelago and which is even said to have a single species in Japan. In the eastern Old World, however, the tropical forms are in a minority owing to the great development of the family in Australia.

Finally, there are a couple of species in New Zealand, and a round dozen in New Caledonia.

The relatively enormous massing of the species of the family in South Africa and in Australia, which is so frequently cited, may be gauged by the statement that about two-thirds of the species are Australian and about one-quarter South African, so that only one-twelfth is left in the whole of the rest of the family area.

The family is divided into two subfamilies, the Persoonioideae and the Grevilleoideae, and the relative distribution of these can be best visualised by saying that the former has no American representatives and that the latter has no African representatives. It will be seen from this that the former is the characteristic group of South Africa, and the latter of Australia. The segregation between the two is, however, not complete, because no fewer than 14 genera of the Persoonioideae are found in Australasia, sometimes in considerable numbers of species.

The family as a whole therefore exhibits (apart from almost indisputable evidence of a southern origin) major discontinuity between Africa and Australia; extension north across the equator in all continents; massing of species in Africa and Australia; minor discontinuity between Australia and New Caledonia and between Australia and New Zealand; well-marked systematic segregation between America and Africa and less marked segregation between Africa and Australia.

The Lobeliaceae

The Lobeliaceae illustrate many points of interest of a rather different kind. In total the family has a very wide range throughout the tropics, and over much of the warm temperate and even temperate parts of the world, but in the latter is

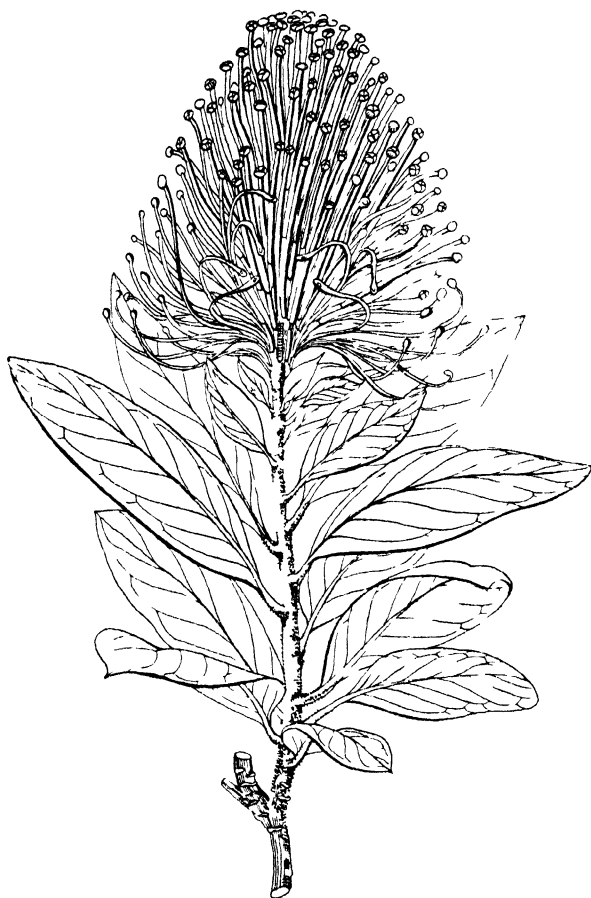


FIG. 14.—*Embbothrium grandiflorum*, a typical member of the Proteaceae, about half natural size, after Baillon

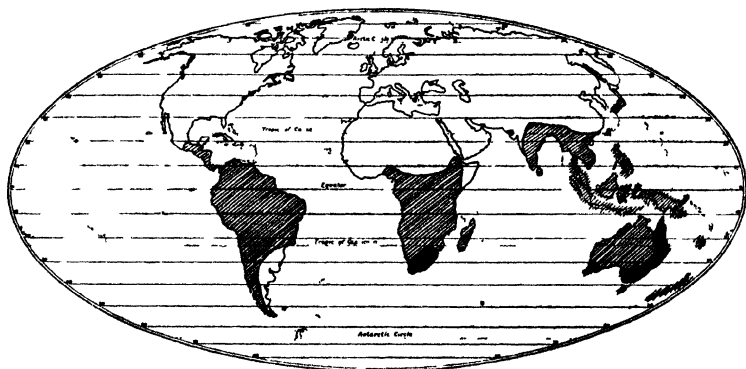


FIG. 15.—Map showing the distribution of the family Proteaceae. The solid black areas are those of greatest species concentration.

represented by comparatively few small herbaceous forms. The main feature of the family is the occurrence in many isolated regions of endemic genera or species with peculiar growth forms, many of which may be described as giant herbs, though some of them are branched shrubs or even small trees.

Lobelia, for instance, which is the central and largest and widest genus of the family, while consisting mostly of herbaceous forms, contains several groups of very distinctive-looking plants. Best known of these, perhaps, are the remarkable columnar giant species which are so conspicuous a feature of the vegetation of the high mountains of tropical Africa (Plate 13), but similar plants are found also in parts of Asia and elsewhere (226). There is also a peculiar shrubby species on St. Helena. In Central and South America, too, there are groups of tall herbs and shrubs.

Very closely allied to the small herbaceous *Lobelias* are a series of genera chiefly in the southern temperate regions and often showing very remarkable distributions. These, however, are almost certainly artificial groups derived from *Lobelia* and may be polyphyletic, so that the geographical facts associated with them must be regarded with caution. They include, however, one monotypic endemic genus, *Brighamia*, in Hawaii.

In the tropical parts of America there are two large genera, *Centropogon* and *Siphocampylus*, consisting of branched shrubby forms, some of which have a climbing habit.

Finally, there are six very remarkable genera of trees, or more commonly shrubs, of various habit with a very noteworthy distribution. Four of them, *Clermontia*, *Rollandia*, *Delissea* and *Cyanea*, are absolutely confined to the Hawaiian Islands, where they are a conspicuous feature of the flora of the mountains and where also they exhibit extreme specific segregation among the different islands. There are also endemic *Lobelias* in Hawaii, and altogether, according to a recent estimate (233), there are in the archipelago no fewer than 150 endemic *Lobelia*-ceous species and varieties.

The other two genera, *Apetahia* and *Sclerotheca*, both very small, are similar in growth form and endemic to the Society Islands.

These peculiar Pacific genera have excited much interest, and their theoretical significance has been discussed at length by Guppy (106) and others.

To summarise, the *Lobeliaceae* show markedly the production of widespread generalised herbaceous forms and extreme endemism associated with marked peculiarity of growth form.

CHAPTER 5

THE DISTRIBUTION OF GENERA—I

WHEN classification was discussed in an earlier chapter, it was pointed out that, from a geographical point of view at any rate, the genus is the most important and illuminating of all categories. The species is, generally speaking, too small a unit to be of much use in the consideration of world-wide problems, and it is moreover an ultimate category not amenable to further statistical analysis. It is encumbered, too, by the confusion arising from the divergence of opinion as to its value. The family, on the other hand, is more often than not too large a category for convenient handling and the total number of families is small. It is, certainly, like the genus composed of constituent units (the genera) and can be analysed in various ways, but the relationship between genera is not even theoretically constant.

The genus, on the contrary, tends to possess the advantages of both the family and the species without their disadvantages. Genera are mostly of convenient size, both taxonomically and geographically, and are made up of constituent parts, the species, which, at least in theory, all possess the same value. Moreover, the conception underlying the genus is very definitely monophyletic, that is to say, the genus more than any other category is presumed to consist of forms closely related not only by structure but also by descent from a common ancestor.

For these reasons genera need special attention, and the next three chapters, which describe their distribution, are to be regarded as among the most important in this book.

Number and Size of Genera

Taxonomically the size of a genus is reckoned by the number of species it contains, and genera vary enormously in this respect. A great many are monotypic, that is to say consist of only one species: at the other extreme are several genera containing upwards of or more than 1,000 species. It is obviously difficult to give definite figures because of the differences of opinion which often exist as to what does or does not constitute a species, just as it is often difficult to say how many genera there are in a given family. There are striking examples of both these points. A recent revision of the family Cruciferae (73) puts the number of genera at over 300, but these are in general so closely similar to one another that the suggestion has even been made that they really constitute only one enormous genus. Again, *Mesembryanthemum* used to be treated as a single genus with some hundreds of species, but it is now (73) generally split up into about 100 genera, most of which are very small. It is important to bear these difficulties in mind because of the constant quotation of figures in this and succeeding chapters. Such quotations are in the opinion of the writer quite essential in order to give some measure of reality and precision to what would otherwise be merely

generalised statements, but all such figures are open to some degree of criticism. It must be remembered, therefore, in perusing them, that they cannot claim to be definitive or absolute and are of value only in so far as they afford a general means of comparison between genera. They can but represent one opinion on what may be, and often are, controversial questions. The figures actually used are taken not only from the writer's own computations, but from various sources, prominent among them being the works mentioned at the end of the Preface.

Estimates of the total number of genera of Flowering Plants known to-day are generally in the neighbourhood of 12,500, and this figure may be taken as a working basis. Computations have also been made from time to time as to the average number of species per genus and the figure most commonly quoted is 12·5. These estimates will receive further attention in Chapter 8.

The largest of all genera appear to be *Astragalus*, with upwards of 2,000 species, and *Senecio*, with about 1,500. *Solanum* is not far behind and is the only other genus with more than 1,000 large species. This reference to large species is necessary because there are genera characterised by extreme polymorphy which results in enormous numbers of very closely similar but slightly different forms. If these are regarded as species, then the genera containing them must be amongst the largest, if not the largest, of all genera. Among them are *Rubus*, *Salix*, *Hieracium*, and *Crataegus*. It is not irrelevant to point out that these genera do seem to depart from the normal in certain respects of their reproduction and genetics so that there may be a real reason for the usual practice of regarding them as special cases.

For the rest there are genera of almost every species number down to the extreme condition of monotypy. These last are particularly numerous, some compilations estimating them at one-third of all genera, while the number of ditypes (two species) is also high, perhaps, according to the same compilations, one-eighth of all genera, so that the two account for about half the total. With increase in species-content so there is decrease in numbers, as is shown by the following figures.

Basing the figures primarily on Willis' estimates (263), and allowing for some more recent increases, it would appear that rather more than 200 genera have from one to two hundred species each, and among the most familiar of these are *Acer*, *Aloe*, *Berberis*, *Buddleja*, *Delphinium*, *Epilobium*, *Eschscholzia*, *Grevillea*, *Hibiscus*, *Jasminum*, *Lupinus*, *Odontoglossum*, *Papaver*, *Rhus*, *Solidago*, *Verbena* and *Viburnum*.

About 100 genera have species numbers estimated between two hundred and five hundred, and familiar examples of these are: *Calceolaria*, *Campanula*, *Clematis*, *Dianthus*, *Eucalyptus*, *Gentiana*, *Gladiolus*, *Heliotropium*, *Impatiens*, *Iris*, *Passiflora*, *Pelargonium*, *Quercus*, *Smilax*, *Trifolium*, *Veronica* and *Viola*.

Only about 25 genera have between five hundred and one thousand species, and these include, roughly in ascending order of size: *Acacia*, *Anthurium*, *Aster*, *Phyllanthus*, *Psychotria*, *Salvia*, *Erica*, *Dioscorea*, *Cyperus*, *Centaurea*, *Eugenia*, *Piper*, *Primula*, *Begonia*, *Dendrobium*, *Euphorbia*, *Rhododendron*, *Ficus*, *Oxalis* and *Carex*.

The figures for *Primula* and *Rhododendron* can hardly be more than provisional estimates, owing to the large numbers of species which have been recently described in these two genera.

It is of some interest to consider the types of distribution exhibited by

these three-hundred-odd large genera and, again on the authority of Willis, this is :

	<i>Genera.</i>
Pan-tropical	78
America only : chiefly tropical	57
Very wide but scarcely cosmopolitan	55
Cosmopolitan	42
Old World : mostly tropical	34
North temperate	19
Tropical Asia ; with some slight extensions	14
America and Africa	8
Australia ; with some extensions	8
Africa	7
Wide Mediterranean	5
South Africa	4
America and Asia	3
North America	2
North America and Mediterranean	2
Eurasia	1
South Africa and Australia	1
South America and New Zealand	1
North America and Eastern Asia	1

Distribution of Genera

The same broad geographical classification which was used for families may be employed for genera, but the size and relative importance of the categories work out rather differently. This is owing, first, to the natural fact that the average range of genera is much smaller than that of families, and, second, to the arbitrary limitation to be attached to endemism. In the families, it will be remembered, endemism was measured in continental terms, but this is much too wide a conception for genera, and something smaller must be taken. Taking the general purpose of this book into consideration, we cannot do better than to interpret generic endemism broadly in terms of the thirty-six regions which were outlined in the floristic classification in Chapter 2. Not only will this provide a suitable conception but it will also serve usefully to throw into relief many features in the floras of these regions. In this account of the distribution of genera then, endemic genera are those which are confined to one only of the floristic regions of the world as outlined in the special scheme given above, or whose ranges are not much greater than the average size of the continental regions therein mentioned.

But with such a conception of endemism it is clear that there will inevitably be many genera which, though too widely distributed to be considered endemic, will nevertheless be far from completely spread through any one major climatic zone. It will be found, on this account, that a category which in the case of the families was almost negligible, namely the "medium wide" category, is in the genera of much greater size and importance, especially from many theoretical points of view. So much so indeed that it must receive very detailed treatment.

Genera may then, for our present purpose, be divided into the following categories :

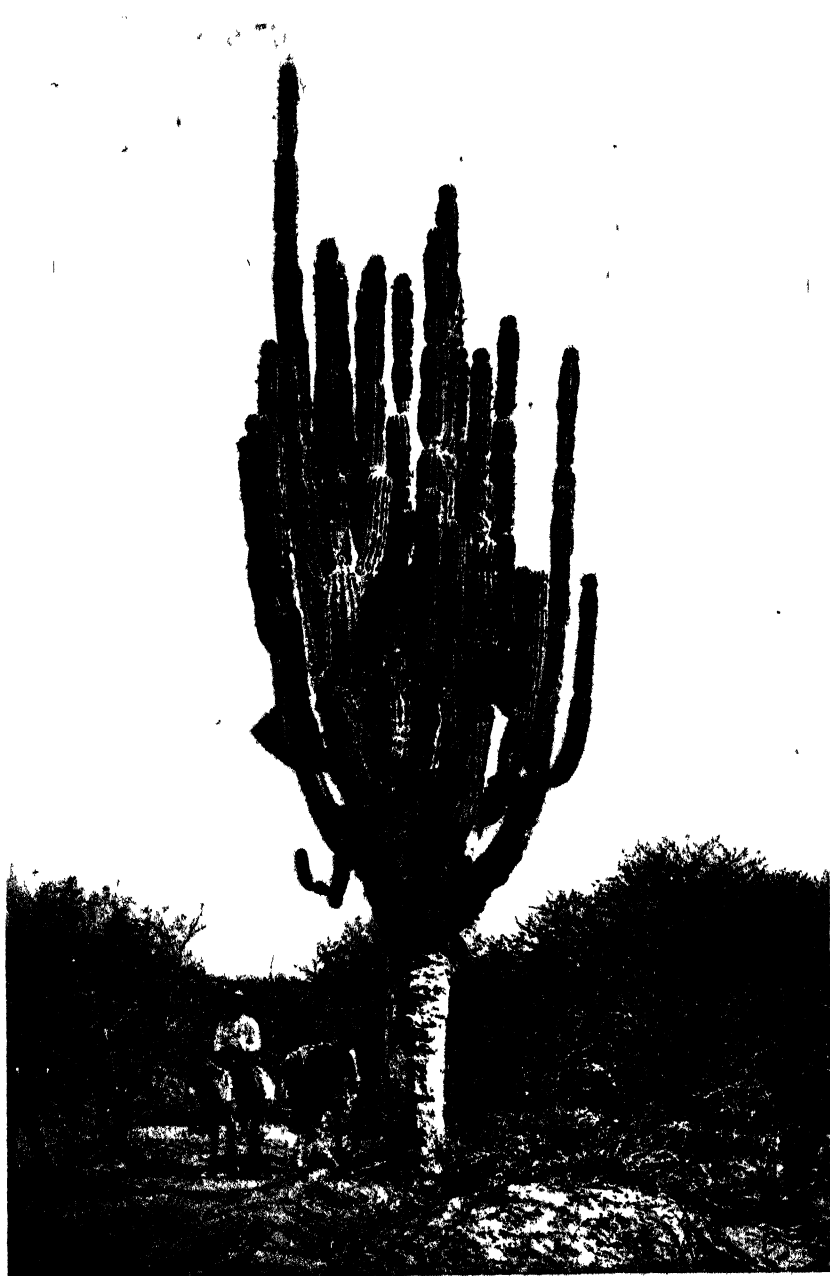


Plate. 6 A Giant Cactus (Pachycereus calvus) in Lower California

(from Karsten & Schenck, Vegetationsbilder)

Cosmopolitan and subcosmopolitan

Tropical

Temperate

Other wides

Discontinuous

Endemic

This arrangement is roughly one of diminishing areas, and it is therefore convenient to take the categories in the order given, as was done for the families. The number of families is such that it was possible to mention each one individually. This is manifestly impossible with the genera, and instead a rough estimate of the number of genera in each category is given together with examples from among the more familiar. In special cases all the genera are mentioned.

Cosmopolitan and Subcosmopolitan Genera

It is usually fairly easy to distinguish between cosmopolitan genera and those with an appreciably less complete distribution, and it is therefore appropriate to divide the whole category on this basis. In each part, too, it will be found that the genera fall into two groups according to their size, and advantage can be taken of this also.

What are here called large cosmopolitan genera consist in all cases of genera with more than 50 species and include some of the largest. They number, including one or two which doubtless owe their completeness of range partly to introduction, 31, namely:

Agrostis, *Anemone*, *Cardamine*, *Carex*, *Centaurea*, *Clematis*, *Cotula*, *Eleocharis*, *Erigeron*, *Euphorbia*, *Festuca*, *Galium*, *Geranium*, *Gnaphalium*, *Hydrocotyle*, *Juncus*, *Nasturtium*, *Plantago*, *Poa*, *Polygonum*, *Ranunculus*, *Rhamnus*, *Rhynchospora*, *Rubus*, *Salvia*, *Scirpus*, *Senecio*, *Solanum*, *Stellaria*, *Teucrium* and *Utricularia*.

Of these *Senecio* is almost certainly the most completely distributed, with numerous endemic species in all parts of the world. *Euphorbia* probably runs it closest. *Carex* is also very widespread but is comparatively scarce in the tropics.

The smaller genera deserving of the term cosmopolitan number less than twenty, and are practically all aquatics. The only marked exception is *Anagallis*, and this genus owes much of its range to introduction. These genera are:

Anagallis, *Apium*, *Callitriche*, *Ceratophyllum*, *Elatine*, *Hippuris*, *Lemna*, *Limosella*, *Ludwigia*, *Myriophyllum*, *Najas*, *Nymphaea*, *Potamogeton*, *Tillaea*, *Wolffia* and *Zannichellia*.

The number of genera so widely distributed as to merit the designation subcosmopolitan is larger, being about 80 in all. Rather less than half are large genera, namely:

Andropogon, *Aristolochia*, *Aster*, *Atriplex*, *Avena*, *Bidens*, *Bromus*, *Chenopodium*, *Convolvulus*, *Cuscuta*, *Cynanchum*, *Cynoglossum*, *Cyperus*, *Drosera* (fig. 16), *Eragrostis*, *Eriocaulon*, *Heliotropium*, *Hypericum*, *Impatiens*, *Lythrum*, *Micromeria*, *Myrica*, *Orobanche*, *Oxalis*, *Panicum*, *Polygala*, *Rumex*, *Salix*, *Satureja*, *Scutellaria*, *Sida*, *Smilax*, *Stachys*, *Stipa*, *Swertia* and *Verbena*.

Of these many, like *Aristolochia*, *Cynanchum*, *Panicum* and *Sida*, are characteristically tropical genera with but a poor and incomplete representation in temperate regions. Others are the reverse, like *Bromus*, *Convolvulus*, *Hypericum*, *Rumex*

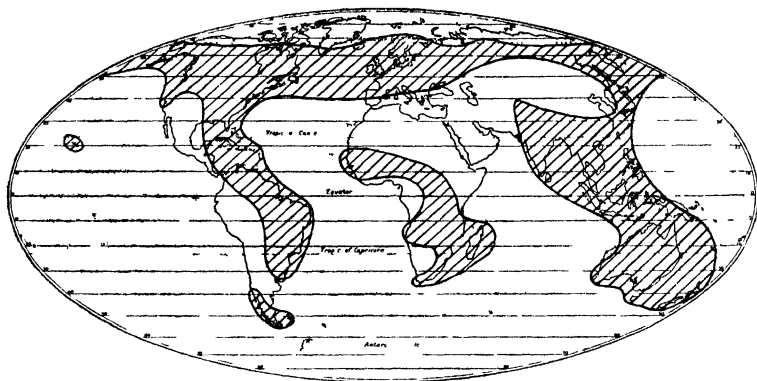


FIG. 16 — Map showing (shaded) the distribution of the genus *Drosera*, after Diels and Irmscher

and *Stachys*, which are characteristically temperate genera, and only sparsely distributed in the tropics. *Orobanche* and *Cuscuta* are parasitic genera. Lastly, some are conspicuously absent or poor in certain parts of the world, while abundant in others, and some of these are in fact to some extent discontinuous. Such, for example, are *Drosera*, *Lythrum*, *Oxalis*, *Salix* and *Verbena*.

Rather more numerous are the small subcosmopolitan genera, of which the following is a reasonably complete list :

Agropyron, *Alchemilla*, *Amaranthus*, *Ammannia*, *Bergia*, *Boerhaavia*, *Brachypodium*, *Briza*, *Calystegia*, *Centunculus*, *Coronopus*, *Cynodon*, *Dactyloctenium*, *Datura*, *Deschampsia*, *Glyceria*, *Gratiola*, *Hordeum*, *Leersia*, *Melica*, *Nesaea*, *Parietaria*, *Paronychia*, *Phleum*, *Physalis*, *Plumbago*, *Polycarpaea*, *Polycarpon*, *Polypogon*, *Portulaca*, *Prunella*, *Rotala*, *Ruppia*, *Salicornia*, *Salsola*, *Samolus*, *Sanicula*, *Spergula*, *Spergularia*, *Suaeda*, *Triodia*, *Typha* and *Vallisneria*.

As before some are mainly tropical, others are mainly temperate, and some are incomplete and more or less discontinuous. In addition this group contains a number of genera like *Salicornia*, *Salsola* and *Spergularia*, which are markedly halophytic.

To summarise, the genera which are so widely distributed that they do not fall conveniently into any of the subsequent categories, and which must therefore be regarded as cosmopolitan or subcosmopolitan, number about 130, the number of large and small genera being about equal. This is not more than 1 per cent. of all genera, and means that very few genera indeed have succeeded in spreading themselves with any degree of completeness over all the land surfaces of the globe. If aquatic genera and special cases like the halophytes are deducted, this point becomes even more striking.

Tropical Genera

Of genera which range practically throughout the tropics of the whole world, there are many well-known examples, but to give a complete list is difficult for several reasons. The published data of distribution, and especially the older ones, are rarely so detailed as to make quite clear the actual extent of distribution in

any or all of the regions concerned. Furthermore, the tropics have their own weed species just as have the temperate regions, and it is often almost impossible to say whether occurrences of these plants are natural or the result of human action. Here these difficulties are surmounted as far as possible by citing as examples only genera in which the facts are generally considered as indisputable. It may also be noted that some degree of incompleteness of distribution over the innumerable islands of the Pacific is not taken as sufficient reason for exclusion from this category.

Although it is not easy to give accurate figures it would appear that about 250 genera are pan-tropical in range. Of these more than 50 have over one hundred species each: rather less than 100 have from twenty-five to a hundred species; and about 100 are smaller still. Among the families the Leguminosae, in the wide sense, are particularly well represented, and grass genera are also numerous, but the status of some of these latter is especially doubtful.

At least twenty of the genera are very small, and the extreme is seen in the monotypic genera *Pistia* and *Sphenoclea*.

Most of the larger genera are fairly well and equally distributed over America, Africa and Asia, as, for instance, *Abutilon*, *Commelina*, *Croton*, *Dioscorea*, *Diospyros*, *Hibiscus*, *Ipomoea*, *Justicia*, *Phyllanthus*, *Piper*, *Strychnos*, *Symplocos* and *Vitex*, but some are more plentiful in one or other continent.

Thus, of genera rather specially developed in America, there may be mentioned *Psychotria* and *Vernonia*; *Ficus* and *Randia* exemplify the fewer cases of Asiatic preponderance; and *Indigofera* illustrates the even rarer condition of African emphasis.

Of genera well developed in two out of the three tropical regions, but which are sparse in the third, are *Acacia*, *Clerodendrum* and *Jasminum*, all common in the Old World but rare in America. The last-named has indeed only one New World species, perhaps introduced.

Begonia is an example of genera relatively poorly developed in Africa: while *Dorstenia* is poor in Asia, having but one species there.

All the foregoing have at least one endemic species in each of the three major regions, but there are some genera, of very varied individual size, which owe their pan-tropical range to the exceptional distribution of one of their constituent species. For instance *Gomphocarpus* and *Microchloa* are, except for one very wide species each, confined to Africa: while *Mikania*, *Jussiaea* and perhaps *Zornia* are, except for a few species, American only. The case of *Mikania* is especially striking because the genus has about 300 species. In all these genera, however, caution must be used, because some of the species are weeds.

It is not to be expected that every genus will fall without difficulty into one or other of the categories listed above, and there are in particular several which serve, by their occurrence partly in one zone and partly in the other, to link up the more characteristically tropical and temperate genera.

Vaccinium (fig. 17), for example, is well developed in the northern temperate zone and is characteristic of many parts of it, but it also occurs more or less all over the tropics. Particularly have many species been described in recent years from New Guinea, and other parts of Malaya also have their representatives. It is least conspicuous in Africa, where it is found only in the east, but this is compensated for by a number of species in Madagascar. It is true also that most of the tropical species are found on mountains, but the genus is nevertheless an excellent example of one with both tropical and temperate forms.

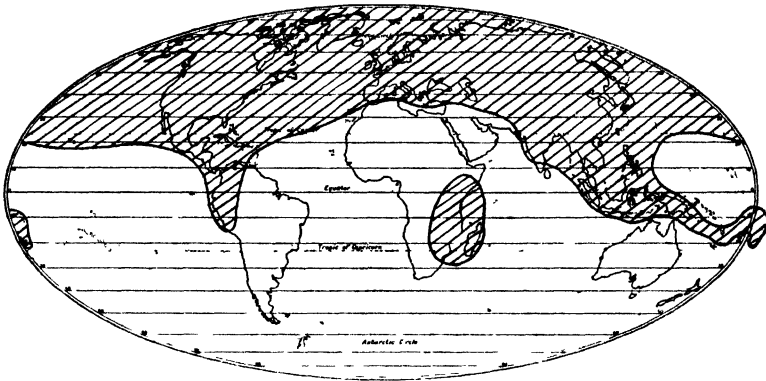


FIG. 17.—Map showing (shaded) the distribution of the genus *Vaccinium*.

The genus *Sedum* is more especially a subtropical or warm temperate genus. It ranges all over the north temperate, but does not reach nearly so far north as *Vaccinium*, and its great centres are in Mexico and the Mediterranean. It has a few extensions into the tropics as in tropical Africa and, less so, in Asia.

Eupatorium illustrates the rather different type of a genus greatly developed in the tropics of one continent (in this case America) and yet circumboreal by the wide extensions of one or a very few of its species. *Anaphalis* illustrates the parallel condition of major development in Asia and one circumboreal species. Here, however, the temperate plant is often adventive and may not be native throughout its actual range.

Temperate Genera

The circumstances of world geography and relief are such that it is difficult to include, in one category, all the genera to which, broadly, the term "temperate" might be applied. For instance genera which are found in all temperate regions are of necessity almost world-wide and have in fact already received notice; while those confined to temperate latitudes are discontinuous, and are dealt with in the next chapter. There remain, however, two great groups of genera which may appropriately be called temperate genera in the narrower sense and which may therefore be considered here. The first of these consists of genera found throughout the northern extra-tropical latitudes, and also to some extent, but incompletely, in the more elevated regions of the tropics, sometimes actually reaching the southern temperate zone. The second consists of genera entirely confined to the northern extra-tropical zone, that is to say, to the northern temperate and arctic regions. Many of the members of these groups will be familiar, at least by name, and it is rather surprising to find that they do not number more than about 165.

The first group can be divided into a number of sub-groups according to detail, and these can be tabulated, with examples, as follows:

1. Genera so widely spread, either naturally or as adventives, as to be almost sub-cosmopolitan :

Cerastium, Epilobium, Luzula, Trifolium, Urtica.

2. Genera with some extensions southwards in all directions, usually to certain tropical mountains only :

Artemisia, Centaureum, Rosa, Thalictrum.

3. Genera extending south in America and Asia :

Prunus, Spiranthes, Vitis.

4. Genera extending south in America and Africa :

Astragalus, Silene.

5. Genera extending south in America only :

- a. Into the tropics—

Cotoneaster, Juglans.

- b. Into temperate South America—

Alnus, Berberis, Draba, Menyanthes, Pinguicula, Ribes (fig. 18), Vicia.

6. Genera extending south in Asia only :

- a. To India or northern Malaya only—

Androsace, Cypripedium, Lihum, Pyrus.

- b. Extension much more marked—

Acer, Quercus.

7. Genera extending to the mountains of tropical Africa only :

Allium, Arabis, Cirsium, Cornus, Subularia.

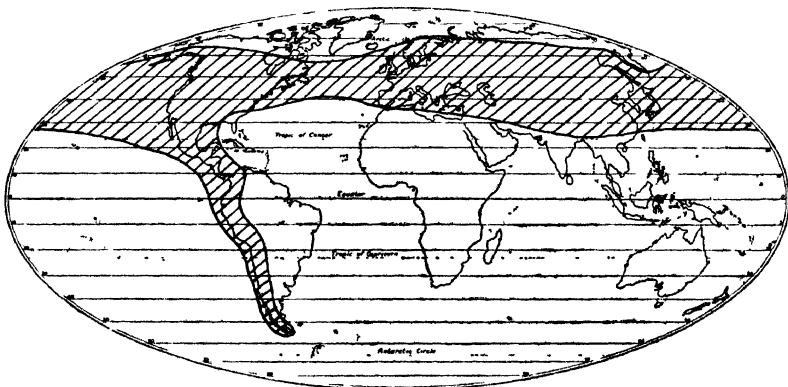


FIG. 18.—Map showing (shaded) the distribution of the genus *Ribes*, after Hutchinson.

The genera which range more or less completely through the northern extra-tropical regions either at all or some latitudes can be divided into three according to the constitution of the genera. First are those in which the species are fairly or very numerous and in which the generic area is much greater than that of any one species. This is by far the largest group, and its 65 genera include many that are familiar. Mostly they call for no special comment and are well exemplified by:

Aquilegia, Epipactis, Fritillaria, Iris, Lonicera, Nuphar, Orchis, Spiraea, Tilia, Trollius.

A few are found in part of North America only, while *Dracocephalum* is a rather special case because only one of its species is American.

Second are the genera with more than one species, but in which one species is circumpolar and accounts for most of the range of the genus. These number about 20 and include *Diapensia, Dryas, and Phyllodoce*. It must be remembered that the range of the more northerly of these species may be small.

Finally, there are the genera such as *Adoxa* and *Loiseleuria* which only have a single circumpolar species.

Other Wide Genera

Under this general heading are included all the continuously distributed genera which are, on the one hand, too restricted to merit inclusion in any of the foregoing categories, but which are, on the other hand, too wide in range to be treated as endemics. Not only are these very numerous, but they show almost every variation in range, so that any cursive account of them would be almost impossible. It is essential, therefore, to tabulate them, and in order to do this they must be classified somewhat rigidly. It is also desirable to give rough figures so that the relative size and importance of the different groups can be appreciated.

Actually there are eight main types of wide, continuous distribution in the sense defined above, and although they can be further divided according to detail it is convenient to arrange their description under these heads. They are:

American wide genera.
 North Pacific wide genera.
 Eurasian wide genera.
 African " "
 Asiatic " "
 Australasian wide genera.
 African-Asiatic-Australasian wide genera.
 Asiatic-Australasian wide genera.

American wide genera

The number of genera confined to America but so widely distributed there as to cover more than one floristic region is about 350, and they fall into the following four groups:

1. Genera more or less completely distributed throughout North America. These number about 70 and include:

Ceanothus, Heuchera, Liatris, Monarda, Rudbeckia and Symphoricarpos.

2. Genera found in North and Tropical America. These number about 40 and include :

Predominantly northern genera—*Helianthus*, *Kalmia*.

Predominantly tropical genera—*Agave*, *Echeveria*.

3. Genera found in tropical and temperate South America. These number upwards of 200 and include :

Alstroemeria, *Ananas*, *Bromelia*, *Escallonia*, *Hippeastrum*, *Mutisia*, *Salpiglossis*, *Tropaeolum*.

4. Genera found throughout America from north to south. These number about 80 and include ;

Cereus, *Echinocactus* (42° N. to 39° S.), *Gaillardia*, *Godetia*, *Helenium*, *Oenothera*, *Opuntia* (from 50° N.), *Petunia*, *Tagetes*.

Some of these genera, such as *Gaillardia*, have minor gaps in their range.

North Pacific genera

The wide North American genera and those of Eurasia are linked up by a small group which are found across and on both sides of the Bering Strait and which may for this reason appropriately be called North Pacific genera. They number about a dozen.

First comes a group of three large genera, *Castilleja*, *Phlox* and *Penstemon*, each with numerous species in the western parts of North America, and with one species in north-east Asia. In *Castilleja* and *Phlox* this latter species is confined to Asia, but *Penstemon* includes one species which ranges from Alaska to Japan. It may be noted that all three genera belong to the same section of sym-petalous Dicotyledons, the Tubiflorae.

Three smaller genera, *Claytonia*, *Anticlea* and *Menziesia*, show a similar massing in North America, with one or very few species in Asia.

Finally, *Chamaerhodos* ranges from Mongolia to western North America ; *Romanzoffia* and *Coelopleurum* are found in north-east Asia and in western North America ; and *Merckia* and *Leptarrhena* are monotypic genera distributed narrowly on both sides of the straits, the former being arctic. *Smilacina* (*Tovaria*) as maintained by Krause (73) may also be included here. It ranges from the Himalayas more or less continuously eastward to Central America.

Eurasian wide genera

Strict adherence to the definition of endemism given earlier would necessitate treating even the genera which range eastward right from the North Atlantic to the North Pacific as endemic owing to the exceptional width of the Euro-Siberian region. A warning was, however, given in Chapter 2 that this region might on account of its size have sometimes to be treated as a special case, and there is good reason for doing so now. Not only are the actual ranges of these genera far greater than those of the average run of endemic genera as defined, but also to call them endemic without qualification is to distort the general picture of plant distribution and to overshadow what is certainly their most important feature, namely, their relatively great longitudinal range and complete occupation of the Old World northern temperate zone.

The number of genera which thus extend right across the great Eurasian

continent north of the tropics and the subtropics comprises, at a rough estimate, about one hundred genera, and among them the families Cruciferae, Gramineae, Compositae and Umbelliferae are conspicuous. At both ends of their range, and more especially in the west, they often show a tendency to extend south into warmer latitudes. The group naturally includes many genera familiar to European botanists either as garden plants or as native wild plants and as far as possible the following examples have been drawn from these :

Convallaria, *Doronicum*, *Eranthis*, *Hedera* (occurs also in Macaronesia), *Lamium* (especially in the west), *Lychnis*, *Neottia*, *Paris*, *Syringa* (especially eastern), *Tulipa*.

African wide genera

Here are included the genera which are widely distributed in Africa (generally with the exception of the north) and in Madagascar, etc. They total between 200 and 300 and are of three main geographical types.

1. Genera found in tropical and southern Africa only. These number more than 100 and include :

Babiana (discontinuous between Socotra and southern Africa), *Euclea*, *Fadogia* and *Voandzeia*, predominantly tropical.

Blaeria, *Protea*, *Stapelia* and *Ursinia*, predominantly southern.

2. Genera found in Africa and in Madagascar, etc. These number about 100 and include :

Myrothamnus in tropical Africa and Madagascar only.

Faurea, *Hydnora* and *Sparrmannia* in tropical and southern Africa and in Madagascar.

Lightfootia and *Selago* with a similar distribution but predominantly found in southern Africa.

Angraecum, *Disa*, *Philippia* and *Stoebe* more or less throughout Africa and Madagascar, etc., *Philippia* being characteristic of the latter and *Disa* and *Stoebe* of southern Africa.

Himantochilus is found in tropical Africa and the Mascarenes only.

Agauria is found in tropical Africa, Madagascar and the Mascarenes.

3. Genera found in South Africa and Madagascar, and occasionally in the Mascarenes. These number about 20 and include :

Alberta, *Cassinopsis* and *Trichocaulon*.

It is very noteworthy that nearly all the genera here represented as in Madagascar or the Mascarenes are found also in South Africa, and that this relationship is, in general, more marked than that between tropical Africa and the islands. It is true that Madagascar, etc., has many genera in common with tropical Africa, but these mostly extend widely also, and therefore, as regards this chapter, appear in other categories.

Asiatic wide genera

This group is a large one calculated to contain between 350 and 400 genera, and is moreover difficult to define numerically because the limits of the genera tend to be in regions where it is hard to trace them accurately. One definite feature, however, is that to all intents and purposes all the genera are limited westward in India, that is to say hardly any range from warm Central Asia to Malaya. Actually three such have been described, namely, *Skimmia*, ranging from Afghanistan to the Malayan Archipelago ; *Sasa*, described as from Central



Plate 7. Puya Raimondii in the Peruvian Andes

(from Weberbauer in Vegetation der Erde)

Asia and Malaya ; and *Myriactis*, ranging from Persia to Java ; but these are so few that they serve only as exceptions that prove the rule.

This fact points the way towards a classification of the whole group into distributional types, which is best done by recognising two main types, the first of which shows ranges from India, China or Japan to the Malayan Archipelago and the second from Burma and Tonkin similarly to the islands. The former are about twice as numerous as the latter.

Each of these main types can be further divided. In the first, by far the largest number consist of genera which range from India only, the Indo-Malayan genera proper. It is probable that these amount to at least 200, and several of the Dipterocarpaceae, such as *Dipterocarpus*, *Hopea* and *Shorea*, are good examples, as are also several other genera containing important timber trees like *Mesua*, *Tectona* and *Walsura*. *Mangifera* seems to belong here as far as its natural range can be ascertained, and other examples are *Colocasias*, *Daemonorops*, *Hodgsonia* and *Osmelia*. A few genera, including *Aporosa*, range eastward from Ceylon and do not occur in the Indian Peninsula proper.

Two other small groups in this main type which are related to the above are genera ranging from India and China and from India and Japan respectively. The first includes *Beaumontia* and *Eriobotrya*, and the second *Camellia*. In *Heterosmilax*, *Michelia* and a few others the northern range includes India, China and Japan.

Finally, there are some genera distributed from China and Japan respectively into Malaya. The former include *Anneslea* and the latter *Broussonetia* and *Cladopus*.

Thladiantha is anomalous in that it is said to range from north Asia to the Archipelago.

The second of the main types exhibits three conspicuous geographical conditions. Most common, and amounting to about 100, are genera ranging from the Malay Peninsula to the Archipelago, and these include *Rafflesia*.

An interesting minor variant of the above is provided by the half dozen or so genera which occur in the Andamans or Nicobars, but not in the Malay Peninsula proper.

Lastly, there is a conspicuous group of twenty-odd genera which range from one part or another of Burma, Siam and Indo-China over the Malay Peninsula and the Archipelago. These include *Barclaya* and *Payena*.

The very interesting subject of the detailed distribution of all these genera within the Archipelago is too complex to be dealt with here in what is but a general survey, but it is worth noting that while many genera occur fairly generally on all the larger islands, an appreciable number tend to be found either in Java and Sumatra or in Borneo or in the Philippines. Of the more generally distributed genera most seem to extend all the way to New Guinea.

At first sight the different groups mentioned above are not easy to visualise, and it is therefore useful to summarise them and to repeat the approximate numbers of genera in each. They are :

1. Genera ranging from India, China and Japan to the Malayan Archipelago, c. 300.
 - a. Genera ranging from India to the Malayan Archipelago, c. 250.
 - b. Genera ranging from India and China to the Malayan Archipelago, c. 15.
 - c. Genera ranging from India and Japan to the Malayan Archipelago, c. 12.
 - d. Genera ranging from China to the Malayan Archipelago, very few.
 - e. Genera ranging from Japan to the Malayan Archipelago, very few.

2. Genera ranging from Burma, Indo-China and the Malay Peninsula to the Malayan Archipelago, c. 150.
 - a. Genera ranging from Burma and/or Indo-China to the Archipelago, c. 250.
 - b. Genera ranging from the Malay Peninsula to the Archipelago, c. 100.
 - c. Genera ranging from the Nicobars or Andamans to the Archipelago, very few.

Australasian wide genera

These are comparatively few in number, probably not more than 60, and fall quite simply into two types, those which are confined to Australia and New Zealand (including the Lord Howe and Norfolk Islands) and those which occur also somewhere in the Pacific Islands.

The first number about 30 and include *Celmisia*, *Persoonia* and *Raoulia*.

Of the rest the genera found in Australia and the Pacific Islands number about 20 and are exemplified by *Ricinocarpus* and *Spiraeanthemum*. Their ranges outside Australia vary a good deal, but for the most part they are restricted to New Caledonia.

The genera of Australia, New Zealand and the Pacific Islands number about half a dozen, among them being *Dracophyllum* and *Epacris*.

Even fewer, among them *Xeronema*, are found in New Zealand and the Pacific Islands only.

Finally, at least two genera, *Carmichaelia* and *Rhopalostylis*, occur in New Zealand and on the Lord Howe Islands.

African-Asiatic-Australasian wide genera

There are included in this very comprehensive category all those genera which, present in Africa, range thence either to Europe and Asia only, or further through Asia into Australasia. From many points of view the category is a very interesting and important one, and must be considered with some care, although any estimate of numbers is difficult for many reasons and especially because it is often impossible to say how continuous a genus is in the desert and semi-desert regions which link Africa and India. As far as can be calculated, the total appears to be about 150.

In general the category comprises two main types of range, namely genera more characteristic of the temperate regions, but with extensions into the tropics, and genera more characteristic of the tropics and reaching all or part of the way from tropical Africa to Australasia and the Pacific Islands.

There must be included in the first of these a rather special group of genera which range from Europe and the Mediterranean southward through Africa. *Adenocarpus*, *Asterolinon* and *Crambe*, with most of their species in the north, are good examples of one extreme and these reach no further than the northern tropics. *Punica* has a rather similar range, but extends well eastward into Asia and its distribution is no doubt confused by long cultivation. At the other extreme are genera like *Erica* and *Gladiolus*, both of which are concentrated in South Africa, but extend up the east side of the continent practically all over Europe and western Asia. Between these extremes are such genera as *Holcus* and *Romulea*, which occur in Europe and the Mediterranean region and also in South Africa, but which appear to be more or less absent in between.

The second main type, consisting of essentially tropical genera, is much larger and can be divided into four. First there are the genera which are practically confined to Africa, but which extend therefrom into Arabia. Here belong *Aloe*, *Catha* and *Kniphofia*.

Next comes the largest group of all, containing genera which range continuously from Africa to India. Some of these, like *Cometes* and *Salvadora*, occur only in the tropical parts of Africa; others, like *Vahlia*, extend to the south of the continent. *Echinops*, *Hyoscyamus* and *Reseda* exemplify genera found in Europe and the Mediterranean as well as in tropical Africa. *Caralluma* ranges from South Africa up the east coast and all over North Africa to India, and lastly such genera as *Hyphaene* and *Delonix* (*Poinciana*) include Madagascar in their distributions.

A third minor type comprises genera of similar distribution, but extending still further into tropical Asia. Examples of these are:

Asparagus, South Africa, Mascarenes to Malaya.

Boswellia and *Cistanche*, Africa to China.

Calotropis, Africa to China and Malaya.

Maerua, Africa, Madagascar and Mascarenes to Siam.

Finally, there are the widest ranging genera of all—those extending from Africa all the way to Australia or the Pacific. It is difficult to estimate the number of these, but they include:

Loranthus, Africa and Madagascar to the Pacific Islands.

Melhania, Africa and Madagascar to Australia.

Viscum, Africa and Eurasia to Australia.

Of all these very varied groups that of the genera ranging from Africa to India is by far the largest, comprising about one-third of the total, but taking the category as a whole there is represented in it almost every degree of distribution from Africa towards Australia and Polynesia.

Asiatic-Australasian wide genera

In one sense this category is the counterpart of the last in that it includes genera with much the same kind of distribution, but with the emphasis on the east and south-east rather than the west. Moreover, although it contains genera which may well have originated in Asia and which have spread thence southward, it certainly comprises many which originated in Australasia and have ranged northward into Asia.

The classification of the category, which in total seems to contain about 200 genera, is into three main groups. In each the genera are represented in some parts of Asia, but in one they occur also in Australasia and the Pacific Islands; in another in Australasia only; and in the third in the Pacific Islands only. Each of these groups can be further divided according to whether the Asiatic distribution includes India, China or Japan, or whether it is limited to Malaya or Indo-China. Moreover, almost every group contains some genera which are predominantly Asiatic and some which are predominantly Australasian, and only in a few cases is there no such distinction.

But this classification is really too complicated for a running description and the facts are best displayed in tabulated form. As previously, the approximate numbers of genera are given and, unless otherwise stated, the word Australia may be taken to mean Australia and/or New Zealand.

Asiatic-Australasian wide genera

1. Genera of Indo-Malaya, Australia and the Pacific Islands :

a. Genera ranging from India and China—

1. Genera predominantly Asiatic, c. 30.
e.g. *Areca*, *Dendrobium*, *Hoya*, *Vanda*.
2. Genera predominantly Australasian, c. 5.
e.g. *Melaleuca*, *Styphelia*.

b. Genera ranging from Malaya—

1. Genera predominantly Asiatic, c. 6.
e.g. *Codiaeum*.
2. Genera predominantly Australasian, c. 15.
e.g. *Grevillea*, *Leptospermum*.

2. Genera of Indo-Malaya and Australia :

a. Genera ranging from India and China—

1. Genera predominantly Asiatic, c. 60.
e.g. *Ailanthus*, *Bambusa*, *Nipa*, *Zingiber*.
2. Genera predominantly Australian, c. 6.
e.g. *Centrolepis*, *Stylidium*.

b. Genera ranging from Malaya—

1. Genera predominantly Asiatic, c. 12.
e.g. *Kentia*, *Myrmecodia*.
2. Genera predominantly Australian, c. 15.
e.g. *Eucalyptus* (fig. 19), *Olearia*.

3. Genera of Indo-Malaya and the Pacific Islands :

a. Genera ranging from India, c. 30.

e.g. *Aleurites*, *Citrus*.

b. Genera ranging from Malaya, c. 25.

e.g. *Metroxylum*.

It may be assumed that all the genera of 3 *a* are predominantly Asiatic, but some of the genera of 3 *b* only extend west as far as New Guinea, and are equally characteristic of the Pacific Islands, often being plentiful in New Caledonia.

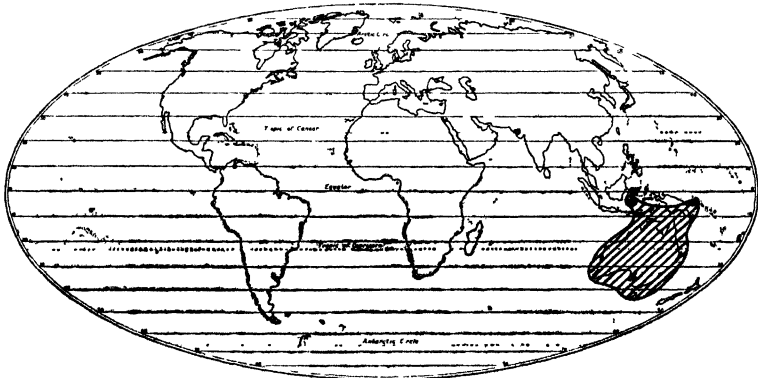


FIG. 19.—Map showing (shaded) the distribution of the genus *Eucalyptus*.

Summary

In order to bring together in conveniently abbreviated form all that has been said in the foregoing pages about the widely distributed genera of Angiosperms, it is desirable to conclude this chapter with a summary of the facts and figures which have been described and discussed. This summary, which comprises all the genera which are neither discontinuous nor endemic, is as follows :

1. Cosmopolitan or very wide genera	c. 130
2. Tropical genera	c. 250
3. Temperate genera	c. 165
4. Other wide genera :	
<i>a.</i> American genera	c. 350
<i>b.</i> North Pacific genera	c. 12
<i>c.</i> Eurasian genera	c. 110
<i>d.</i> African genera	c. 250
<i>e.</i> Asiatic genera	c. 370
<i>f.</i> Australasian genera	c. 60
<i>g.</i> African-Asiatic-Australasian genera	c. 150
<i>h.</i> Asiatic-Australasian genera	c. 220
Total	c. 2050

From this table it therefore appears that about 15 per cent. of all genera may be regarded as wide genera, leaving about 85 per cent. for discontinuous and endemic genera.

CHAPTER 6

THE DISTRIBUTION OF GENERA—II

Discontinuous Genera

THE facts of discontinuous distribution are among the most remarkable in all the geography of the Flowering Plants and on this account alone would demand special attention here, but there is a second and related reason why a careful survey of them is particularly desirable. Discontinuity is a matter which bears upon many problems (especially those concerning the distribution of land and climate in the past) beyond the confines of botany, and it has therefore, not unnaturally, attracted the attention of many who are not botanists, and their statements regarding it are not always to be taken at their face value. Thus there has arisen a certain amount of confusion regarding the facts, and a general survey which reviews the subject as critically as possible may serve also to dispel some of this. Since the story of discontinuity in general is largely the story of generic discontinuity in particular, this chapter comprehends the most important part of such a survey.

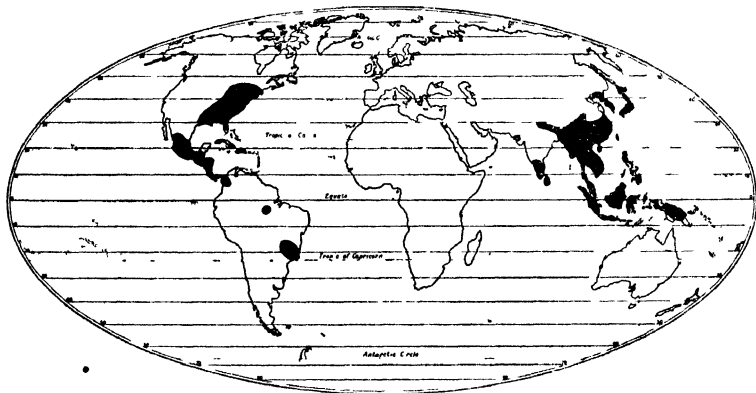


FIG. 20.—Map showing (black) the distribution of the tribe Magnolieae.

When one plant group is found distributed over two or more widely separated regions its discontinuity is significant, in theory at all events, only if it can be assumed that its range was formerly continuous and that the subsequent disjunction has resulted from natural causes. Expressed rather differently, discontinuity is of interest, from most points of view, only when it can be assumed that the group exhibiting it is of monophyletic origin and has therefore had not only a common ancestry but also a single point of origin. It is by the quotation, as discontinuous, of genera which do not fulfil these conditions that confusion has chiefly arisen.

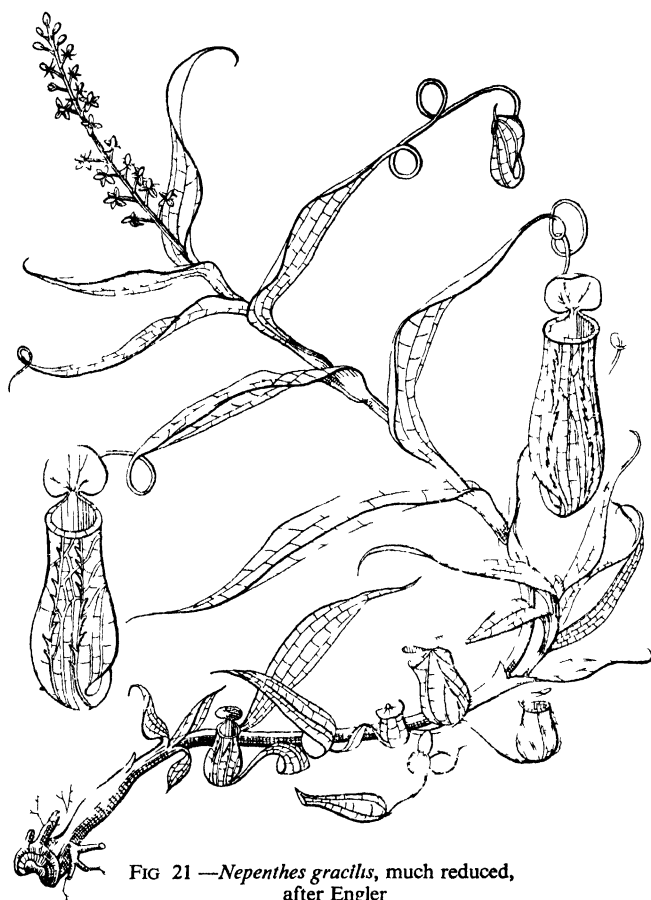


FIG 21 —*Nepenthes gracilis*, much reduced,
after Engler

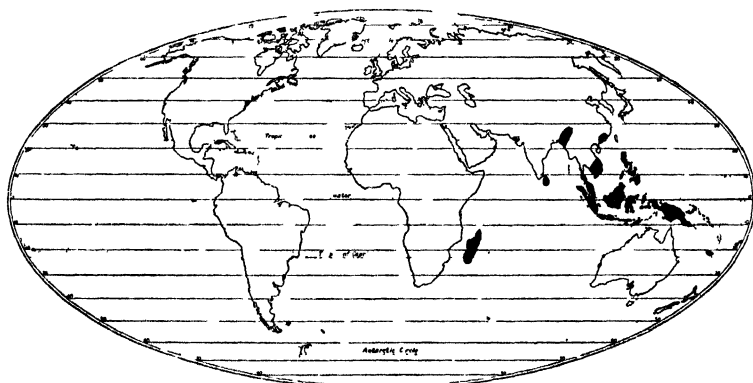


FIG 22.—Map showing (black) the distribution of the genus *Nepenthes*, after Hutchinson

The greatest difficulty lies in deciding which genera are to be regarded confidently as monophyletic groups, because here the only possible criterion is that of personal opinion, but there are two types of genera which must almost certainly be excluded. The first comprises those which consist of two or more very distinct subgenera separated by characters which in other cases are often regarded as of full generic value. Not uncommonly such genera are described as discontinuous because each of the subgenera has a distinct range, but if the relationship between them is open to doubt, so also of course is their discontinuity, and reference to it is merely misleading.

The second case is much commoner and especially concerns certain large and particularly "natural" families. In these families the constituent species are all so much alike that it is very difficult to group them into separate genera and it becomes necessary, in order to do so, to emphasise and rely too rigidly upon characters so detailed and minute that their value as criteria of true relationship can only be described as very doubtful. Thus in some families especially the genera as commonly defined can but rarely be accepted as monophyletic units. This is true, for instance, in the Compositae, where one of the most prevalent types of generic distinction is the minute morphology of the style arms; and, again, in the Acanthaceae, where minor characters of the anthers are much used. Sometimes, of course, other and more practicable features come into play, but the general result is that nearly all the discontinuities recorded for these and a few other families must be treated with reserve.

Another common difficulty is that of deciding whether or not a plant is of natural occurrence in all parts of its range. The heather and certain heaths, for instance, are often quoted as striking examples of wide discontinuity on the strength of their occurrence in eastern North America, but investigation shows that they are by no means free from the suspicion that the American plants are in fact intentional or unintentional introductions from the Old World and that they do not, therefore, confer discontinuity in the phyletic sense on the genera to which they belong. Sometimes years elapse before cases of this kind can be determined, and this is why the discontinuity of the Bromeliaceae, based on the recorded occurrence of the genus *Pitcairnia* as native in Africa, has been treated above as still *sub judice*.

Misidentifications and errors of fact also lead to misunderstanding. Slips of the pen or tongue have frequently attributed to genera discontinuity which in fact they do not possess. In collecting plants and in dealing with them subsequently data sometimes get misplaced: these errors may eventually pass into print, and once this has happened it is not at all easy to correct them. As regards identification, a wrong conclusion regarding to which of two genera a new species belongs may lead to great geographical confusion.

It was the realisation of these difficulties that prompted the present writer, some years ago, to review all the genera which had from time to time been described as exhibiting wide discontinuity, that is to say discontinuity of approximately continental or oceanic dimensions, and to compile a list of those which could with reasonable confidence be looked upon as good and reliable instances of it, omitting those which for such reasons as have just been mentioned were to be regarded at least with suspicion. In short, the object of the review was to produce a list of all the genera which could be safely quoted as examples of widely discontinuously distributed monophyletic groups. This list appeared in 1927 (92), and at the time the hope was expressed that a revised edition might be published at a later



FIG. 23.—*Hibbertia volubilis*, about natural size, after Baillon.

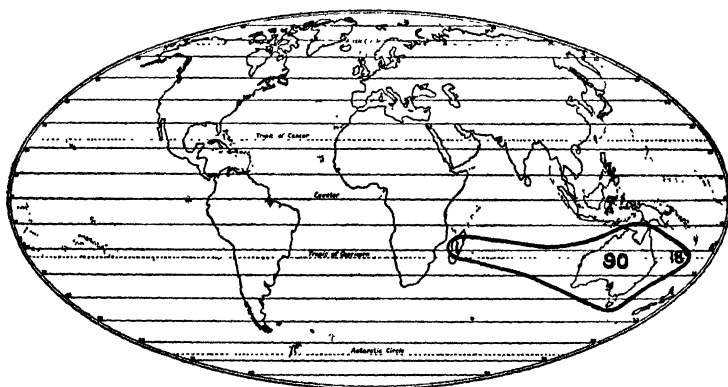


FIG. 24.—Map showing the distribution of the genus *Hibbertia*. The three figures are the numbers of the species in the different parts of the range.

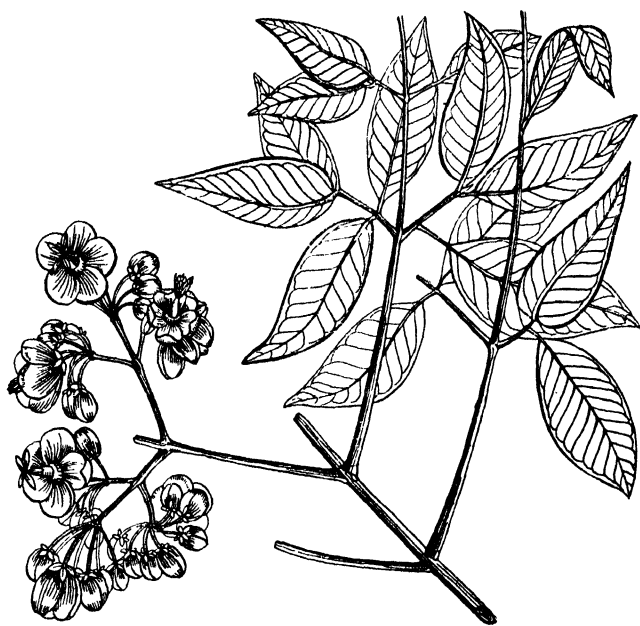


FIG. 25.—*Symphonia globulifera*, about half natural size, after Engler.

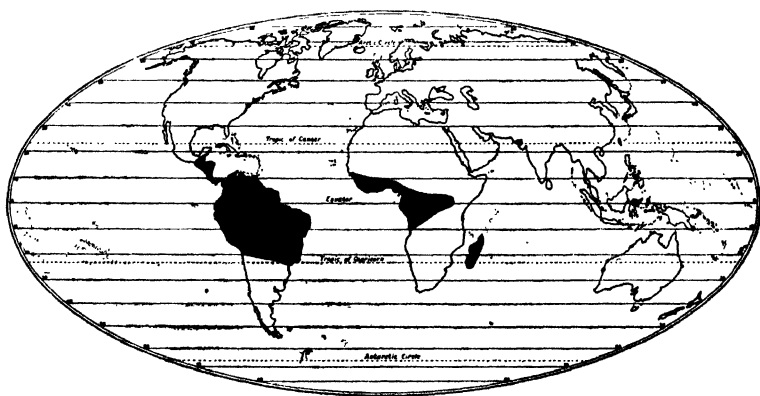


FIG. 26.—Map showing (black) the distribution of the genus *Symphonia*, after Hutchinson.

date. This book now furnishes the opportunity for this, and a second edition of the list is given with the necessary explanatory notes in Appendix B. This course of printing the list separately has been adopted because to have incorporated it in the text of this chapter would have overburdened this with detail and would have made the cursive reading of it almost impossible. The following pages include, however, a more generalised account of the list and of the classification and figures that it presents, and the Appendix can be used to amplify this as may be felt desirable.

The distribution of land and sea and the zonation of climate are such that the discontinuous genera of the Flowering Plants are of five main types, *i.e.* :

1. Genera entirely or predominantly confined to the northern temperate regions.
2. Genera entirely or predominantly confined to the tropical zone.
3. Genera entirely or predominantly confined to the southern temperate regions.
4. Genera occurring in both northern and southern temperate regions.
5. Genera of various distributions, but all occurring in the exceptionally isolated Hawaiian Islands.

The northern temperate discontinuous genera comprise, as might be expected from the huge extent of this area, several very distinct types, including some which range over the whole of it and rather fewer which occur at both ends of the Eurasian continent, but the commonest discontinuities are between America and Europe and America and eastern Asia respectively.

The last is one of the most familiar and important of all and, from the time that Asa Gray (102) first drew special attention to it, has been much studied and discussed. These genera number about eighty and there is reason to believe that they may be survivors of a very ancient circumboreal flora which has failed to survive in Europe and western Asia. They can be further classified according to the details of their Asiatic distributions, some occurring only on the continent ; some in Japan ; and others in both. Some of them, moreover, have marked extensions southward into the tropics of one or both hemispheres.

The total number of genera in this northern temperate category is about 125, and the following are some of the best examples of them :

- | | | |
|----------------------|---|--|
| <i>Liquidambar</i> . | . | According to most authorities there are three species—one in North and Central America, one in south-western Asia, and one in Formosa and south China. |
| <i>Meconopsis</i> . | . | Taylor (239) regards this genus as consisting of one western European species and about forty in the Sino-Himalayan mountain system. Some taxonomists include also two western North American species. |
| <i>Corema</i> . | . | A genus of two species—one in North America from Newfoundland to New Jersey and the other in the Azores, the Canaries, Spain and Portugal (fig. 38). |
| <i>Platanus</i> . | . | There are four species in western North America and Mexico, one in eastern North America, and one in the eastern Mediterranean and in Asia Minor. Seward (213) gives an interesting map of the past and present range of this genus. |
| <i>Clintonia</i> . | . | This genus has six species—two in western North America, two in eastern North America, one in the Himalayas and one in east Asia. |

- Menispermum* . . . According to Diels (69) there are two species—one in eastern north America and one in north-east Asia, north China, Korea and Japan.
- Liriodendron* . . . One of the most striking and often quoted instances of discontinuity. There is one species in eastern North America and one very narrowly distributed in eastern China (Plate 18 and fig. 63).
- Chiogenes* . . . There is one species throughout eastern North America and one in Japan. Some consider the latter to be only a variety of the former.
- Magnolia* . . . According to Dandy and Good (111) there are some species in eastern North America and a larger number in eastern Asia, both groups having an appreciable extension into the tropics (fig. 20).
- Nelumbo* . . . According to Irmscher (137) one species extends from the Caspian to Japan and through Malaya to Australia and a second from North America to Brazil (figs. 65, 66).

The tropical genera considered here as discontinuous comprise those which, while not completely pan-tropical, nevertheless occur in two or more of the main land divisions of this zone. Whether or not it is to be interpreted as a measure of the relatively great age of the tropical flora as a whole, the fact remains that the genera of this category are far more numerous than those of all the others put together, amounting indeed to nearly two-thirds of the total.

The three most obvious subdivisions are composed of genera found in America and Africa (e.g. figs. 25, 26), in America and Asia, and in Africa and Asia (e.g. figs. 27, 28) respectively, but not all the genera which have to find a place can be included in these, and it is necessary to recognise two further groups, one of genera more widely, but still discontinuously and incompletely, distributed over the tropics (e.g. figs. 29, 30), and one to include still more anomalous cases.

Of the three first divisions that of the African-Asiatic genera is more than twice as large as the other two together, and in this connection it is relevant to remind the reader that this is the only case in which the two constituent land masses are actually contiguous. Of the two divisions involving the New World that of the American-African genera is nearly three times as large as that of the American-Asiatic and Australasian groups.

The two divisions involving Africa can each be further classified according to whether the genera occur on the continent only; on the continent and on Madagascar, etc., or on the islands only. Specially remarkable is the small but distinct group of genera which are found in America and elsewhere only in Madagascar.

The actual ranges of these various types are sufficiently indicated by the titles of the divisions to which they belong and it is unnecessary to quote many examples of them apart from three of which figures and maps are given here. These are:

- Nepenthes* . . . A well-known genus of pitcher-plants with more than fifty species ranging from South China to New Guinea, and in addition one species in New Caledonia, one in the Seychelles and one in Madagascar (figs. 21, 22).
- Cunonia* . . . A genus with about a dozen species in New Caledonia and one in South Africa. The latter is illustrated in fig. 6 and the distribution of the genera of the Cunoniaceae in fig. 7.
- Hibbertia* . . . In some respects like the last, but much larger. There are nearly one hundred species in Australia, about fifteen in New Caledonia, and one in Madagascar (figs. 23, 24).



FIG. 27.—*Ancistrocladus Heyneanus*, about half natural size, after Engler.

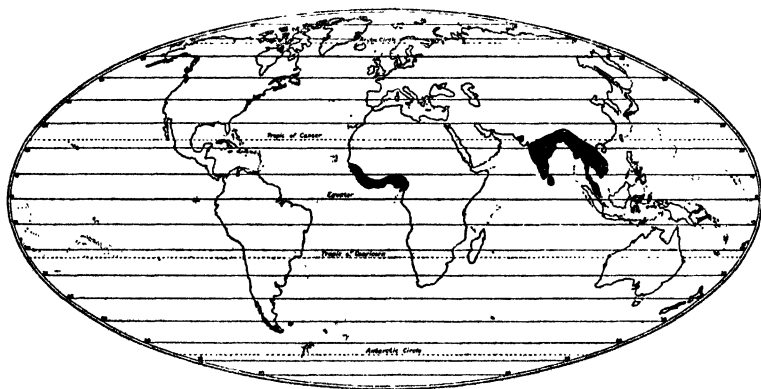


FIG. 28.—Map showing (black) the distribution of the genus *Ancistrocladus*, after Hutchinson.



FIG. 29.—*Hernandia peltata*, somewhat reduced, after Seemann.

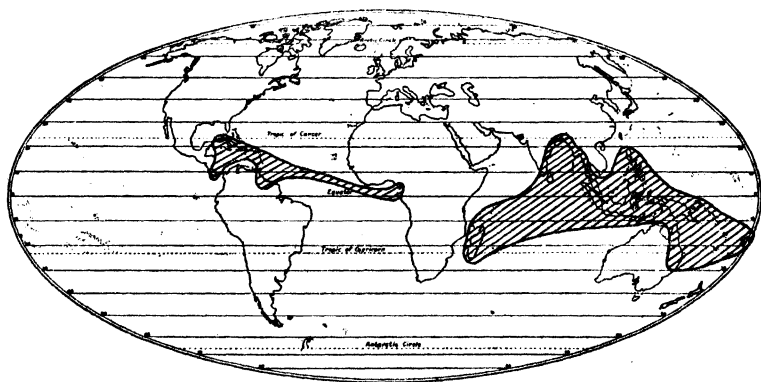


FIG. 30.—Map showing (shaded) the distribution of the genus *Hernandia*, after Hutchinson.

The more widely ranging discontinuous genera of the tropics are by the nature of the case much more miscellaneous and admit of no general description. Some idea of their details will, however, be apparent from the following which are some of the more outstanding of them :

- Clethra* . . . This genus is almost confined to America and Asia, but one species occurs on Madeira (figs. 31, 32).
- Turnera* . . . There are many species in tropical America, and in addition one that ranges from the Seychelles and Réunion to Indo-Malaya.
- Kalanchoe* . . . A large genus with all but one of its species in the Old World. The exception is a plant found locally in Brazil. It is usually described as distinct and as a native, but it is possibly adventive.
- Styrax* . . . Very like *Clethra* in that all but one of its species are American or Asiatic, but the exception in this case is found in the Mediterranean region.
- Weinmannia* . . . A large genus with the great majority of its species in tropical America, but it is also fairly well distributed in Madagascar, etc., as well as in Malaya and the Pacific Islands, and there are one or two species in New Zealand (fig. 6).

The anomalous discontinuous genera of the tropics are even more miscellaneous and nearly every one of them has its own particular interest, and at least the following call for special reference here :

- Aldrovanda* . . . A monotypic aquatic genus recorded from the warmer parts of Europe, north-east Asia, India, Japan, central Africa, Timor and Australia.
- Brasenia* . . . Also a monotypic aquatic genus and rather like the last except that it occurs also in the New World. It has been recorded from Manchuria, India, Japan, Australia, tropical Africa and from North and Central America.
- Cohnia* . . . This genus has been recorded from the Mascarenes and from New Caledonia. This is a very extraordinary range and the relationships of the genus need further study, but it is notable that a somewhat similar distribution is attributed to some other genera, and particularly to the next.
- Cossinia* . . . This genus has been credited with exactly the same range as the last and the same remarks apply. It may again be emphasised that these are not the only genera showing relationship between the Mascarenes or Madagascar and New Caledonia.
- Kissenia* . . . According to Dandy (51) this genus is found only in southern Arabia and Somaliland and in the south-western part of South Africa. The plants in the two areas are much alike and may represent only one species.
- Pelargonium* . . . A large genus with the great majority of its species in South Africa, whence it extends to Madagascar and up the east coast of Africa to Arabia and western India. There are also several species in Australia and one occurs in Australia, South Africa and on the Tristan da Cunha islands.
- Pharnaceum* and *Hypertelis* . . . Together these form a natural group of species almost entirely confined to Africa and Madagascar, but with one, now very rare, on St. Helena.
- Phylla* . . . Very like the last, but occurs on Tristan as well as on St. Helena.

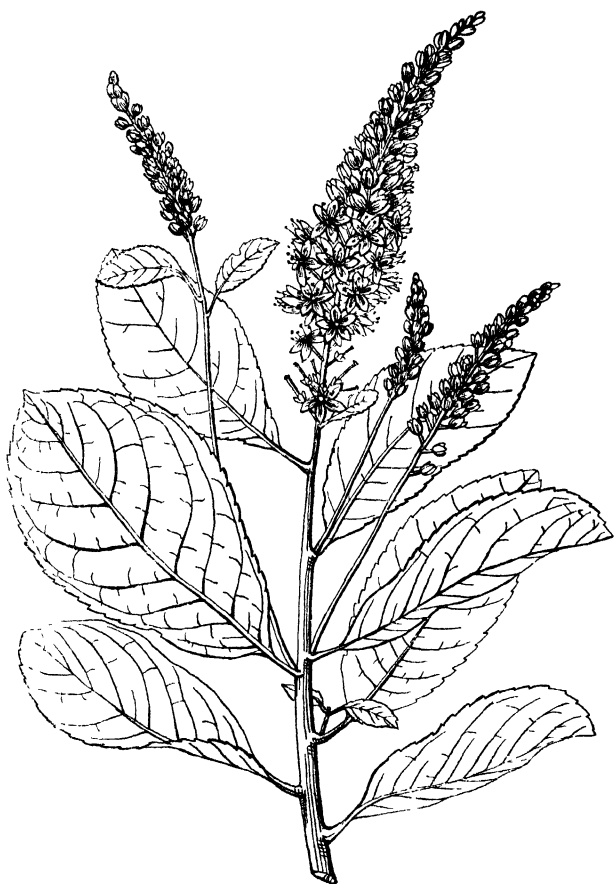


FIG. 31.—*Clethra arborea*, about natural size, after Bailey.

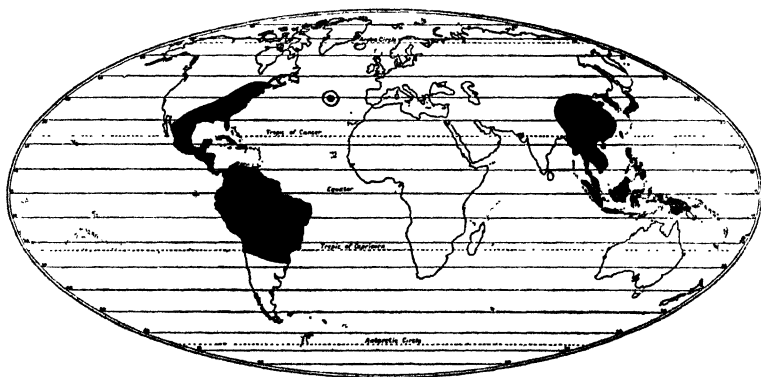


FIG. 32.—Map showing the distribution of the genus *Clethra*, after Irmischer.

It will be remembered that of the three land extensions south from the north circumboreal belt those in America and in Asia and Australasia are much longer than that in Africa, and it is, therefore, not surprising to find that among the discontinuous genera of the southern temperate regions (e.g. figs. 33, 34) (which number some fifty in all) those confined to America and to Australasia are much the most numerous. Some are confined to Africa and Australasia, but other types are scarcely represented. A very few are anomalous.

The genera of the first of these groups are of special interest and importance in relation to the past history of the Antarctic continent and have been much studied in this connection. The writings of Skottsberg in particular (see bibliography) on this subject are of first importance and should be consulted by all who are interested in the great problems they involve.

These genera can be further subdivided according to whether they are found in Australia and New Zealand or in only one of these. The first condition is, with eighteen genera, much the commonest, and that of occurrence in Australia only is the rarest.

The general features of these southern temperate genera are fairly adequately displayed by their classification, but the following may be noticed in detail as specially noteworthy examples of the group:

- Colobanthus* . . . Most of the species are confined to New Zealand, but one is common to New Zealand and Australia. There are also at least two ranging from New Zealand to South America and occurring also on many of the South Temperate Oceanic Islands.
- Lilaeopsis* . . . A genus of rather problematical species constitution and according to Hill (122) recorded from North America, Mexico, Bolivia, Chile and the Falklands as well as from Australia, Tasmania and New Zealand.
- Nothofagus* . . . This genus contains the southern beeches, and although usually kept distinct is closely related to *Fagus*. It has about a dozen species in Chile and Fuegia, about half a dozen in New Zealand, two in Australia and one in Tasmania (fig. 33).
- Fuchsia* . . . Most of the species occur in America and especially in the tropical parts, but there are two or three, including *F. procumbens*, in New Zealand.
- Jovellana* . . . A genus closely related to *Calceolaria* and having a range very like that of *Fuchsia*, with one or two species in Chile and a few in New Zealand (fig. 33).
- Phyllachne* . . . This genus has three species in New Zealand and one in Fuegia, the latter being the only member of the family (Stylidiaceae) in the New World (91) (fig. 3).
- Drimys* . . . Most of the species are in the eastern part of the Malayan Archipelago and especially in New Guinea, but there are others in Australia and in parts of South and Central America (fig. 5).
- Restio* . . . A large genus confined to South Africa and Australia and well represented in each. The family to which it belongs (Restionaceae) has, in general, much the same distribution.
- Carpobrotus* . . . This is one of the modern segregates of the large genus *Mesembryanthemum*. It has about a dozen species in South Africa, several in Australia and one in Chile.

Pringlea

"The Kerguelen cabbage", a monotypic genus once thought to be confined to the island group of that name but now known also from Heard Island, Marion Island and the Crozet. It thus combines very wide discontinuity with a very small actual area of occurrence

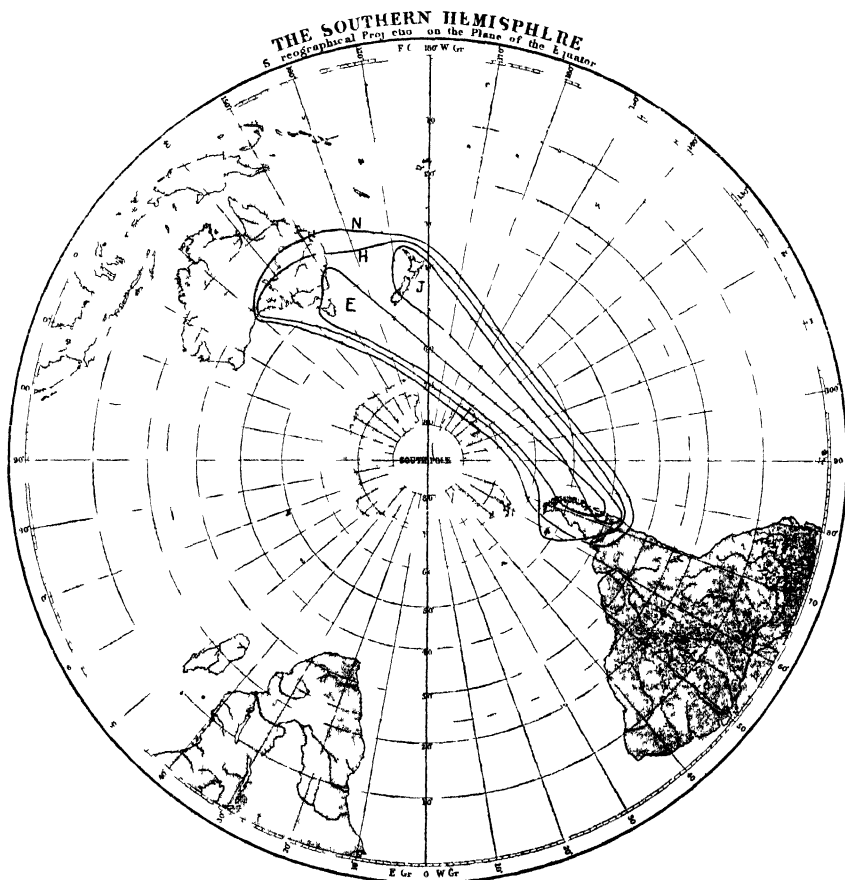


FIG 33 — Map showing the distribution of the genera

N *Nothofagus* after Berry and Fernald,

H *Hebe* after Berry and Fernald,

J *Jovellana* and E *Eucryphia* after Hutchinson



FIG 34 — *Eucryphia glutinosa*, about natural size, after Hutchinson

The fourth great category, of genera found only in the north and south temperate zones, is particularly hard to estimate because of the difficulty of determining the real status of many plants which occur more or less naturally in the temperate parts of the southern hemisphere. Frequently plants which seem, at first sight, to be native there, turn out on further investigation to be, in all probability, adventives, and therefore not to be reckoned as authentic cases of discontinuity. There is also the problem of deciding which of the many genera that extend with more or less marked gaps along the Andes are in fact sufficiently discontinuous to merit inclusion. When these two difficulties in particular are allowed for, the number of genera in the category appears not to exceed about sixty.

These are best further divided according to their ranges below the equator. Some occur, for instance, in all three parts of the southern hemisphere, others in only two out of three, and still others in only one. In all there are seven possible combinations and of these six occur, the only case of which there appear to be no examples being that of distribution in the northern temperate zone and in South America and South Africa. The commonest state is that of occurrence in the north and in South America only, and this is doubtless correlated with the exceptional ease of migration along the great line of the Rockies and the Andes. Details

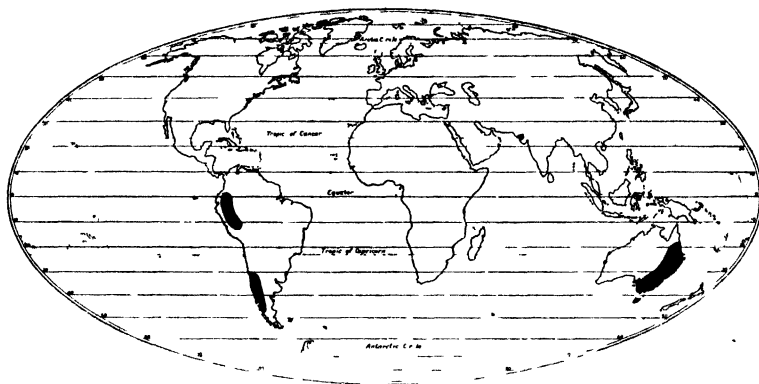


FIG. 35.—Map showing (black) the distribution of the genus *Lomatia* (Proteaceae), after Imscher.

of the numbers in each of these several types must be sought in the Appendix, but the following may be cited as specially interesting examples of the category as a whole :

- Frankenia* . . . The wide total range of the genus (137) is due to the extensive distribution of a single species which is found more or less continuously from Europe to Central Asia and through Africa to the Cape, but there are also a number of other species in the Mediterranean region. Besides these there is a large group of species in Australia, another in Chile, and a smaller one in western North America. The genus is also recorded from St. Helena.
- Myosurus* . . . A very small genus found in the northern temperate zone and in all three parts of the south temperate regions.
- Coriaria* . . . The only genus of its family and one of the most remarkable examples of discontinuity (95). The few species occur in tropical America, Chile, the Mediterranean region, eastern continental Asia, Japan and New Zealand. In addition at least one species is found both in South America and in New Zealand (figs. 36, 37).
- Papaver* . . . Almost entirely a northern genus and centred in the Mediterranean region, but there is one species in South Africa and Australia.
- Oligomeris* . . . There is one fairly widespread species in the northern temperate regions and about seven in South Africa.
- Damasonium* . . . Two species occur in the Mediterranean region and there is one in the southern half of Australia.
- Empetrum* . . . Another very remarkable instance of discontinuity (93). It is a genus of two species and is completely circumpolar in the north. Elsewhere it is found only in temperate South America, including the Falklands, and on the Tristan group (fig. 38).
- Honkenya* . . . Widely distributed in the northern temperate regions and occurs also, apparently native, on the coast of Patagonia. It is a monotypic genus but its subspecies and forms are also completely segregated geographically.

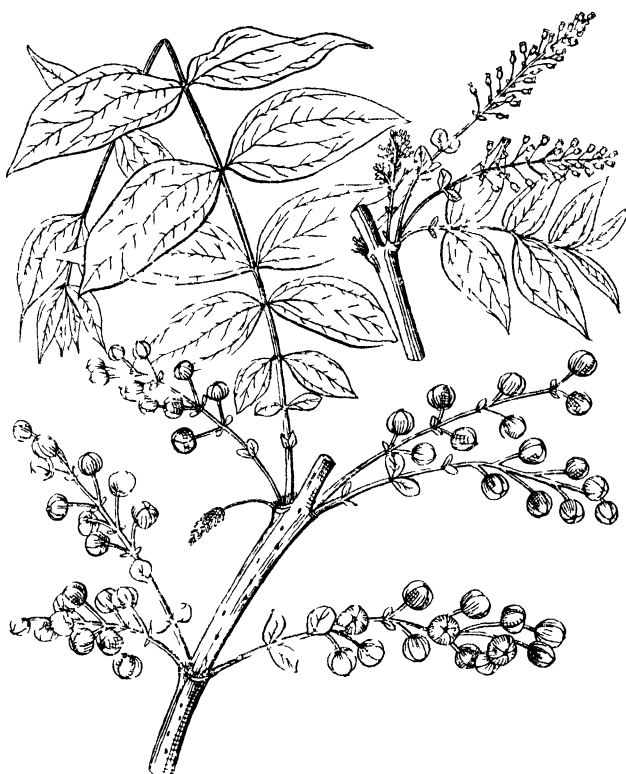


FIG. 36.—*Coriaria japonica*, about half natural size, after Bailey.

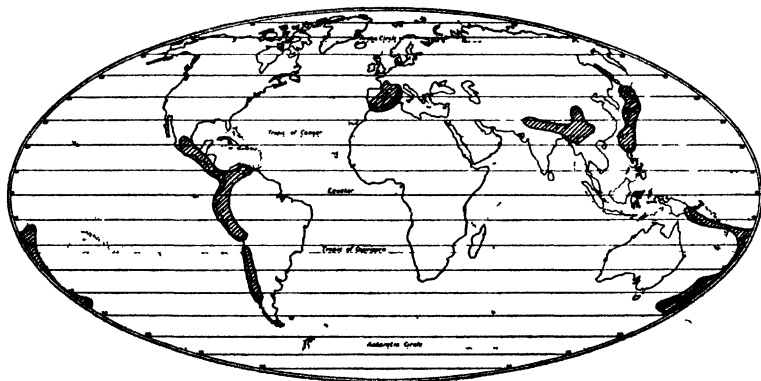


FIG. 37.—Map showing (shaded) the distribution of the genus *Coriaria*.

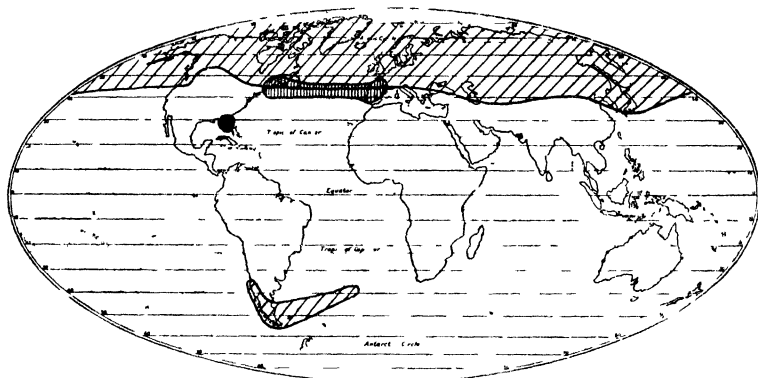


FIG. 38.—Map showing the distribution of the three genera of the family Empetraceae:—
wide diagonal shading—*Empetrum*,
close vertical shading—*Corema*,
solid black—*Ceratiola*.

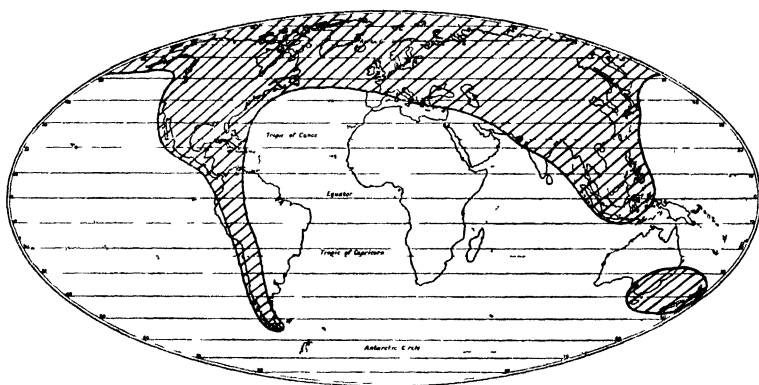


FIG. 39.—Map showing (shaded) the distribution of the genus *Gentiana*, after Irmscher.

Littorella . . . A genus of two species, one of which is found in Europe and in eastern North America and the other in Patagonia. It thus combines two distinct types of discontinuity.

The last of the five categories, that which concerns certain plants found in the Hawaiian Islands, is scarcely comparable with the others but it is, nevertheless, of considerable interest. It is made necessary by the extraordinary isolation of these islands and by their position roughly equally distant from Asia and America. As will be seen later, these islands have a great number of endemic genera and their flora also includes many which are cosmopolitan, pan-temperate or pan-tropical. The forty-eight genera which comprise the present category are therefore those genera of the flora which, outside the islands, have a fairly restricted distribution and which thus are of special interest as a clue to the general affinities of the flora.

In this connection it is most noteworthy that of these genera thirty are found elsewhere only in the Old World, compared with only about half a dozen found in the New World. The residue are found in both. The category as a whole includes some genera with very remarkable distributions, and in particular the following deserve notice :

Coprosma . . . According to Oliver (178) this genus is massed in New Zealand and in Hawaii, but it is found also in Australia, Malaya, the Pacific Islands and on the Juan Fernandez group (figs. 40, 41).

Pittosporum . . . A large genus found throughout the tropics of the Old World and also in Hawaii.



FIG. 42.—*Astelia montana*, somewhat reduced, after Seemann.

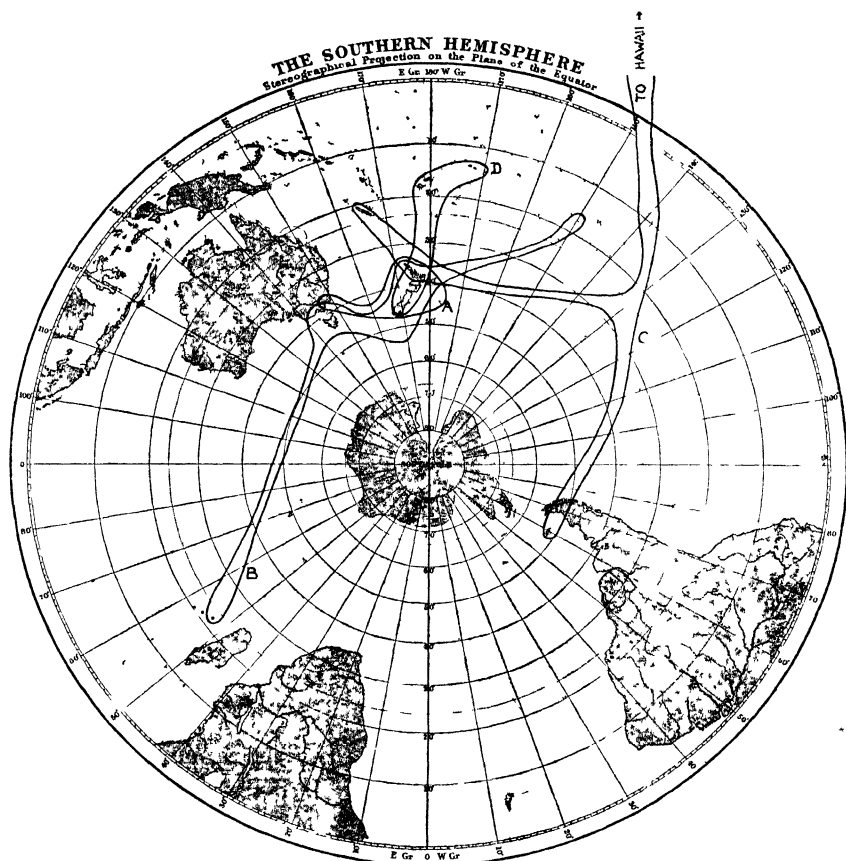


FIG. 43.—Map showing, A, B and C the distribution of the three sections of *Astelia*, and D the closely allied genus *Collospermum*.

- Cuphea* . . . Another large genus, exclusively American except for one species which reaches not only the Galapagos Islands but also Hawaii.
- Astelia* . . . According to Skottsberg (228), there are six species in Hawaii, one in the Marquesas, one in Tahiti, one in Samoa, one in Fiji, one in New Caledonia, one in New Guinea, three in Australia and Tasmania, fifteen in New Zealand, one in Réunion and two in Fuegia (figs. 42, 43).
- Nertera* . . . A genus centred in New Zealand and with some representation in tropical Asia. It includes also one very widespread species recorded also from Australia, Tasmania, Hawaii, South America and Tristan da Cunha.

Gunnera . . . According to Skottsberg (230) the genus is chiefly South American with a minor group in New Zealand having a slight extension into Malaya. It occurs also in Africa and Madagascar, and in Hawaii (Plate 9, fig. 44).

The complete list as given in Appendix B contains about 750 genera. For the reasons given earlier this is almost certainly an appreciable underestimate of the total number of discontinuous genera in the Angiosperms, and hence it can at least be said that these amount to more than 5 per cent. of all genera. Among them tropical genera predominate strongly.

It would be particularly interesting to calculate the number of discontinuous genera in the different families, but the method of classification of certain families makes it almost impossible to do this. It is, however, possible to calculate the relative and absolute frequency of the different families represented in the list, and this reveals some interesting facts.

The Leguminosae, using the term in its comprehensive sense, is the most frequent family and is followed in the order named by the Compositae, Euphorbiaceae, Rubiaceae, Liliaceae, Scrophulariaceae and Apocynaceae. Taking into account what has been said about the Compositae in particular, the number here is remarkably high and indicates that, as might be expected from its size, this family probably actually has more discontinuous genera in total than any other.

It is more interesting to note that, as the list stands at present, some of the smaller families show by far the highest *proportion* of widely discontinuous genera. Saxifragaceae, Gentianaceae, Sterculiaceae, Rutaceae, Olacaceae, Meliaceae, Oleaceae, Rhamnaceae, Aizoaceae, Simaroubaceae, Combretaceae and Rhizophoraceae, for instance, have very high figures, but even these are exceeded by the Magnoliaceae and, above all, by the Berberidaceae. In the last indeed practically every genus finds a place somewhere in the list, and this fact, if it is not already sufficiently realised, may well attract the special attention of students of this family.

Mention of the Rhizophoraceae, the family containing the mangroves, serves as a reminder that one very special kind of discontinuous distribution has received

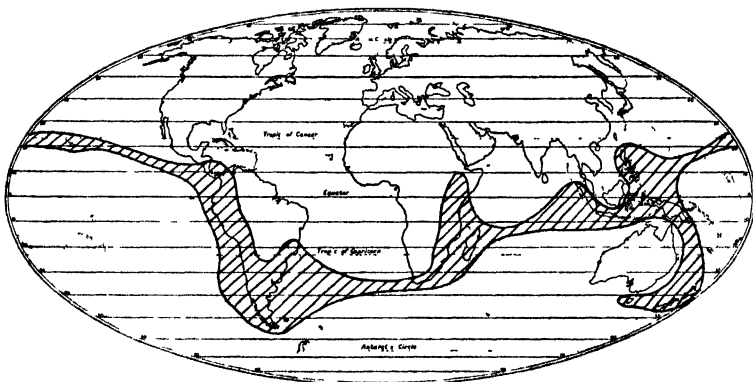


FIG. 44.—Map showing (shaded) the distribution of the genus *Gunnera*.

practically no notice above. This is the discontinuity which is generally and indeed almost inevitably shown by wide ranging plants whose habitats are in, or closely associated with, shallow marine waters.

Such plants fall into three groups, namely, the marine Angiosperms, which live actually submerged in the sea ; the mangroves, which inhabit muddy tidal shores ; and certain so-called strand plants, which grow either on, or just inland of, sandy shores. Each of these groups contains many genera which are discontinuous and form a conspicuous element in at least the tropical category of the list given in Appendix B. It is clear, however, that their discontinuity is of a very particular and special kind, and for this reason and also because it is, more often than not, a matter of individual species, more detailed consideration is deferred to a later chapter, where it will be described at some length.

CHAPTER 7

THE DISTRIBUTION OF GENERA—III

Endemic Genera

ENDEMIC genera have been, for present purposes, defined as genera either actually confined to one floristic region or having distributions not greatly exceeding the average size of a region. This latter qualification is necessary because many genera, while comparatively restricted in range, actually extend over parts of two regions. On the other hand, many are so local as to occupy much less than the whole of an average region.

Taking into account the figures already given for other categories, it would appear that about 10,000 genera are endemic in the sense just defined, and for the purposes of the short and formal survey which is all that is possible here they can be dealt with most conveniently if they are classified according to the thirty-six regions which form the basis of the floristic arrangement used here. Here and there it is necessary for special reasons to depart from this treatment, but on the whole it not only permits the easy handling of this great mass of genera but also provides a useful opportunity for drawing attention to special features of interest in the floras of these regions.

As far as possible figures are again quoted, but they are intended only to give some idea of relative numbers. The various examples selected for mention are, whenever possible, those most likely to be familiar to the general reader.

It should also be borne in mind that the inclusion of a genus in any particular regional account does not necessarily mean that it is exclusively confined to that region but only that the region in question is that of which it is most characteristic. Many genera naturally extend somewhat beyond the limits of the region in which the bulk of their range and the majority of their species occur.

Arctic and Sub-arctic Region

The arctic provides an excellent instance of the limitations to the use of endemism in estimating floristic rank, because, though all authorities are agreed that the arctic flora is a sufficiently distinct entity to be reckoned as a major unit in floristic classification, it has, in fact, practically no endemic genera. A few, including *Arctagrostis* and *Parrya*, have been described as such, but they are small and not too well defined.

It is in this negative quality that the chief interest of the arctic flora lies, because the proportion of endemics tends to increase with the degree and duration of isolation. There is good reason to believe that the arctic flora, in its present form, is one of the youngest and perhaps the youngest in the world. It also shows a minimum amount of isolation, consisting indeed merely of the most resistant elements of the northern temperate flora and their derivatives. The boundary between the two indeed is a purely subjective one.

It should also be borne in mind that the arctic region, except for Greenland, which is almost covered by an ice-cap, is a small one and that the polar region proper is occupied by the Arctic Ocean.

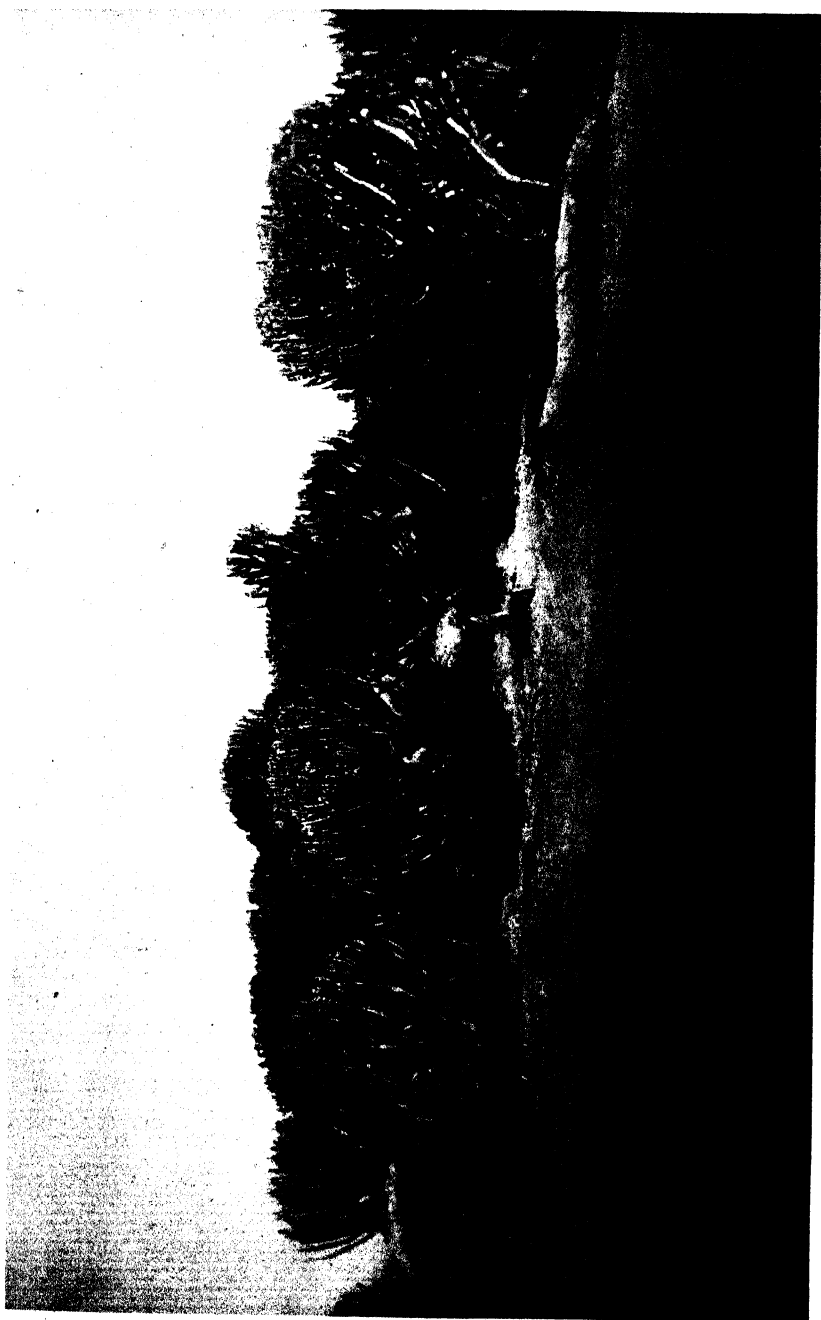


Plate 8. *Euphorbia abyssinica* in Eritrea; a Specialized African Type of a Cosmopolitan Genus

(from Karsten & Schenck, *Vegetationsbilder*)

Euro-Siberian Region

It was found convenient to deal with the genera which range throughout this exceptionally extensive region in the last chapter, and attention is here confined to genera which are endemic to one or other part of it.

The total number of these is probably between one and two hundred, and as these are conspicuously massed either at the European or Siberian ends of the region, they may be dealt with under these heads.

The western genera, namely those of Europe only or of that continent and parts of west Asia, certainly number more than half the total. The former group contains about fifty genera and includes *Aethusa*, *Daboecia* (*Dabeocia*), *Lunaria*, *Melittis* and *Pulmonaria*. All are small, and the last named, with some dozen species, is perhaps the largest. Also confined to Europe and actually even more localised are some twenty genera found only in one or more of the mountain systems. These include *Erinus*, *Nigritella*, *Ramonda* and *Soldanella*.

The genera which range over Europe and nearby Asia are fewer but contain such familiar examples as *Astrantia*, *Dictamnus*, *Digitalis* (which reaches Macaronesia), *Eremurus*, *Laburnum* and *Vinca*.

The flora of north-east Asia is less rich than that of Europe and, rather naturally, much less well known. It is also scarcely isolated from that of north-west America, and partly as a result of this the number of endemic genera is small, examples being *Bergenia*, *Caragana* (reaches west Asia), *Codonopsis* and *Rheum* (reaches Syria).

Sino-Japanese Region

This region consists of three main parts—the elevated area of the Sino-Himalayan-Tibetan mountains; the rest of China; and an insular area, Japan. The flora is, on the whole, homogeneous throughout except that the inclusion of the whole Himalayan complex brings in extraneous elements to some extent. To regard these mountains as a single whole, however, makes for a very useful simplification and does not obscure any very salient facts.

The total number of endemic genera in this very considerable region is almost certainly several hundreds, but it is difficult to give figures because new plants are still being discovered in it. Whatever the figures are, the genera divide fairly simply into groups.

A few range over almost the whole region, among them *Aucuba*, *Caryopteris* and *Hovenia*. More are found in both China and Japan and thus cover nearly the whole area, and these include *Callistephus*, *Paulownia* and *Rehmannia*.

Genera confined to China number well over a hundred and may be many more, but it must be remembered that the southern part of the country belongs to another region. Chinese genera include *Kerria*, *Litchi* and *Poncirus*.

Similarly the southern part of Japan is outside the region and this makes it difficult to estimate the number of its endemic genera. Willis (263) lists about seventy for the whole country, but other sources indicate a lower figure. One genus at least, *Fatsia*, is familiar.

The Himalayan system is the native home of many highly prized garden plants, but its endemics do not number much more than 100, most of its characteristic genera having wider ranges. Among the better known examples are *Davidia*, *Leycesteria* and *Nomocharis*.

Several genera, while massed in the Himalayas, extend somewhat out of the region, as, for instance, *Cremanthodium* (94), which can only be included here by stretching a point, as one or two of its more atypical species reach well into Tibet and north China. *Meconopsis* also is essentially a Himalayan genus but actually, on account of a species in Europe, discontinuous.

On the south the region shows considerable linkage with its neighbours. A number of genera are, for instance, described as ranging from India to Japan, and in another direction a handful of genera extend south towards Malaya, among them being *Aspidistra* and *Schizophragma*.

Western and Central Asiatic Region

This region, which comprises the Caucasus, Armenia, part of Persia, part of Russia, and part of Tibet, as well as the rather indeterminate countries between east Europe and China, is difficult to deal with because its limits bear little relation to political boundaries, a point which always complicates the investigation of plant distribution. It consists of dry mountainous areas or of actual deserts which are often salt, and the vegetation is comparatively limited and specialised.

As far as any estimate can be of value it appears to contain about 150 endemic genera, and these are almost all small and specialised. Halophytes and xerophytes are well represented, and more than a third of the total belong to the Cruciferae, a family of notoriously difficult generic distinction. Chenopodiaceae and Umbelliferae are also plentiful, and these three families together account for more than half the total.

Most of the genera are fairly well distributed, but some, like *Dorema*, are restricted to the western part and others, like *Tetraena*, to the east.

Cannabis and *Spinacia* are almost the only very familiar genera. The former, as far as its native range can now be determined, is confined to the region, but the latter extends into Mesopotamia. *Exochorda* extends eastwards into China, and *Phelipaea* is a true endemic parasitic genus.

Mediterranean Region

The actual area of land within this region is small, being confined, except for the larger part of the Iberian Peninsula, to the littoral zones of the Mediterranean, and it has a very specialised type of vegetation, which is reflected in a high proportion of endemic forms. Furthermore, the boundaries between it and the neighbouring regions are not always clear and many genera characteristic of the Mediterranean in fact extend far beyond it. This is specially noteworthy in the north, where many Mediterranean genera range far up into western Europe and some actually reach the British Isles, where, as will be seen later, they form an important element in its flora. Among these are *Anthyllis*, *Atropa*, *Bellis*, *Bryonia*, *Hippocrepis*, *Jasione*, *Medicago*, *Ophrys*, *Origanum*, *Tamus*, *Ulex* and *Verbascum*.

Among others, generally represented in Britain by garden plants only, are *Centranthus*, *Crocus*, *Galanthus*, *Gypsophila*, *Helleborus*, *Lavandula*, *Muscari*, *Narcissus* and *Nigella*.

Including these the total number of Mediterranean genera is probably over 250. Among them *Aethionema* and *Cistus* stand out as exceptionally large genera, the

former having more than fifty species. The latter, though rather smaller, is perhaps the most characteristic of all Mediterranean plant groups because it contributes so largely to the peculiar type of vegetation known as the "maquis." Among other fairly well known examples are *Aubrietia*, *Galega*, *Malope*, *Phillyrea*, *Pisum*, *Rosmarinus* and *Santolina*, all of which range fairly widely over the region.

As examples of rather more restricted genera there may be mentioned—*Helxine* on Corsica and Sardinia; *Triplachne* on Sicily; *Astrocarpus* in Spain; *Argania* and *Zilla* in North Africa; and *Drosophyllum* in south Spain and neighbouring North Africa.

There are also a few genera, mostly Umbelliferous, recorded only from Syria.

On the east side the region connects up with Central Asia by several genera such as *Chionodoxa*, *Cicer* and *Danae*, but it is difficult to classify genera here, because while parts of the coast of Asia Minor belong floristically to the Mediterranean region the interior belongs to Central Asia.

On the west side the region shows relationship with Macaronesia in the presence of several genera, including *Ruscus*, which occur in both.

Macaronesian Transition Region

The degree of generic endemism in this region is low and chiefly of interest in relation to its distribution among the island groups. In all there are less than thirty endemic genera.

Of these nearly twenty are confined to the Canaries, including *Phyllis*, *Plocama* and *Semele*. Five are confined to Madeira. Two only are found on the Cape Verdes, and there is none on the Azores.

Of the rest three inhabit the Canaries and Madeira; *Lytanthus* is in the Canaries and the Azores; and *Aichryson* ranges over the Canaries, Madeira and the Azores.

It should be noted that most of these genera are in the islands nearest the mainland, and that the most isolated group has no endemic. It is also noteworthy that the region as a whole has a latitudinal range of 20 degrees.

Atlantic North American Region

The endemic genera of this region probably number between one and two hundred. It must, however, be remembered that many genera characteristic of eastern North America extend right across the continent and have, therefore, been considered among the wide genera in Chapter 5.

Some of the endemics, like *Baptisia* and *Robinia*, are almost extensive enough to rank as wides, but there are others which are very narrow. *Franklinia* is a particularly interesting case because it appears to be one of the few genera which have actually become extinct in a wild state during the historical period. One single plant of a single species was discovered in the eighteenth century on the Atamaha River in Georgia (80), and from this tree the existing garden individuals are all descended. The original wild tree, however, has disappeared and apparently no other has ever been seen.

Among other interesting genera confined to the Atlantic States of North America are *Ceratiola*, *Dionaea*, *Sanguinaria* and *Sarracenia*.

Pacific North American Region

Various estimates go to indicate that there are at least several hundred endemic genera in this region. The richest part is certainly California, but many genera extend nearly all over it. It is, however, safe to say that the number is greater in the south than in the north.

Eschscholzia and *Abronia* are good examples of wider endemics, while *Sidalcea* and *Tolmiea* exemplify genera of the more northern parts. Others, chiefly of the south, are *Choisya*, *Darlingtonia* and *Romneya*. *Sarcodes* is a remarkable saprophytic plant from the Sierra Nevada.

As is usual, a number of genera mainly characteristic of the region show transition with its neighbours. *Yucca*, for instance, though characteristic of the south-western U.S.A., extends widely east in the southern part of its range. *Bigelovia*, similarly, has one species in the east. *Zinnia*, again, is centred in the southern part of the region but has one species which extends right down to Chile. *Garrya* reaches Mexico and the West Indies.

North African—Indian Desert Region

This region, though very extensive, has, as might be expected from the nature of its climate, a comparatively restricted vegetation, and the number of its endemic genera almost certainly does not much exceed fifty and may be less.

Some of these genera are widespread, as is *Londesia*, which actually connects this region with that of Central Asia, since it ranges from Arabia to Mongolia. *Cornulaca* stretches from the Sahara to Mesopotamia. *Fortuynia* and *Zataria* are eastern genera ranging from Persia to Afghanistan.

Among more restricted endemics are *Mecomischus* from the Sahara; *Xerotia* from Arabia; *Duthiea* from north-west India; and *Salvia* from Aden.

Endemic Genera of Tropical Africa

This is one of the points at which it is convenient to depart from a rigid regional classification, because the different regions into which tropical Africa is divided are so closely related that a large number of genera are not markedly confined to one of them although they are endemic to the tropical parts of the continent. They therefore can scarcely rank as wides, and must receive notice here.

These more extensive endemics probably do not number more than two or three hundred and most of them are small, although *Ritchiea*, for instance, has upwards of fifty species. They include *Cola*, *Erythrocephalum*, *Khaya*, *Monotes*, *Ocotea*, *Oricia*, *Pleirotaxis* and *Ricinodendron*.

Some are confined to the mountains and occasionally show some discontinuity. *Thunbergianthus*, for instance, is recorded from the island of St. Thomas in the Gulf of Guinea and from Ruwenzori; and *Pseudagrostistachys* from St. Thomas, Fernando Po and the Ruwenzori region.

Even with the more narrowly distributed endemic genera of tropical Africa it is convenient to modify the regional classification slightly and in two instances to combine together a pair of separate regions. These pairs are the Sudanese Steppe Region and the West African Forest Region, and the North-east African Highland and Steppe Region and the East African Steppe Region, respectively.

By reckoning these four as two double regions an important point is emphasised, namely the occurrence of two well-marked floras, one covering what may be called western tropical Africa and the other eastern and southern tropical Africa, and the advantage of doing this outweighs the drawback of departing from the more rigid regional arrangement, and also simplifies the presentation of the relevant facts.

Sudanese Park Steppe Region and West African Rain-forest Region

The total number of endemic genera in these two portions of the African continent appears at present to be about 200 odd, but knowledge of the flora here has increased in late years and this may well prove to be an underestimate. Whatever the number may be, however, there is no doubt that the majority of them belong to the forest rather than to the steppes, and those of the latter are relatively few, chiefly because their flora is mainly part of one which covers much of the African tropics.

Moreover, except to the specialist, the genera are not very familiar and there need only be mentioned *Carpodinus*, *Maesobotrya*, *Napoleona* and *Oldfieldia*.

Several genera, including *Heteradelphia* and *Principina*, are confined to the small islands in the Gulf of Guinea.

North-east African Highland and Steppe Region and East African Steppe Region

Taken together these two regions represent eastern and southern tropical Africa, and reach from south Angola to the Red Sea. The north-east part divides very clearly into two areas, the highlands of Abyssinia and the lowlands of Eritrea and Somaliland. The flora of the first is closely related to the rest of tropical Africa, while that of the second is more nearly allied with that of the North African—Indian desert region.

The total number of endemic genera in this double region is probably of the order of 250, with the same reservation as in West Africa.

The north-east region does not account for more than about fifty of these, and nearly half of this group are confined to the island of Socotra, which for its position has a remarkably peculiar flora.

The rest are fairly evenly divided between Abyssinia and Somaliland, examples of the former being *Afrodivella* and *Hagenia*, and of the latter *Drakebrockmania* and *Poskea*.

Oreophyton and *Edithcolea* range southward into East Africa proper, and *Morettia* connects the region with that of the African-Indian deserts.

The endemic genera of the rest of east and southern tropical Africa are practically all small and unfamiliar and scarcely form a conspicuous element in the flora. This is due chiefly to the great mingling of floras which has taken place here, and especially to the extension northward in East Africa of many genera more particularly characteristic of the southern parts of the continent.

The more strictly endemic genera are for the most part found either on the east side of the continent or in Angola and northern South West Africa. The former include *Saintpaulia* (*S. ionantha* is a not unfamiliar greenhouse plant) and *Synadenium*, and among the latter are *Corynanthe* and *Umbellulanthus*.

East African Island Region

This region comprises Madagascar and its small islands ; the Comoros between Madagascar and the mainland ; the Seychelles to the north ; and the Mascarenes to the east.

The total number of endemic genera is probably rather more than 200 and the great majority, certainly over 150, are found on Madagascar itself or, as is the case in a few small genera, on the very tiny islands close to it.

The most striking element in the endemic flora of Madagascar is that of the seven genera which make up the endemic family Chlaenaceae, and of which *Rhodochlaena* is perhaps the chief. Among other endemics are *Bembicia*, *Boutonia*, *Hydrotriche*, *Stapelianthus* and *Vomitra*.

Certain genera like *Dicorypha* and *Ravena* are found on both Madagascar and the Comoros, while a few others, such as *Cremocarpus*, are confined to the latter.

Lomatophyllum and *Poupartia* exemplify a small group of genera which range over Madagascar and the Mascarenes. Apparently *Brandzeia* is the only genus confined to Madagascar and the Seychelles.

The endemics of the Mascarenes number about thirty and are variously distributed. Thus, *Cylindrocline* and *Roussea* occur on Mauritius ; *Hyophorbe* and *Pyrostria* on Mauritius and Rodriguez ; *Mathurina* and *Scyphochlamys* on Rodriguez ; *Fargesia* and *Guya* on Réunion.

There are about a dozen endemic genera in the Seychelles. *Medusagyne*, which is confined to a single island, forms an exceptionally local family, while *Deckenia* and *Lodoicea* are noteworthy genera of palms.

Region of Ascension and St. Helena

In area this is probably one of the smallest of all the regions, comprising only two small islands. Its natural flora is also extremely small to-day because the rich native vegetation of the larger island has gradually become almost exterminated. There is, however, still enough left to show that the original flora was almost entirely distinctive and peculiar. The degree of specific endemism indeed must have been very high, although the number of endemic genera was perhaps not considerable.

To-day there are known only five endemic genera, all from St. Helena. They are *Melissea*, *Petrobium*, *Nesiota*, *Commidendron* and *Melanodendron*, the last two exemplifying the woody members of the Compositae which are, and still more were, a feature of the flora.

South African endemic genera

Once again, in the case of South Africa it is desirable to depart from the regional classification. Two regions cover the southern part of the African continent, but they are very different from one another. The Cape region, which actually constitutes a separate floristic kingdom, consists only of the south-west part of the Cape Province and is thus one of the smallest continental regions, but it has one of the most remarkable and perhaps the richest of all the world's floras. It is also of special interest because it has contributed much to the beauty of European gardens. The South African transition region, on the other hand, has not a particularly rich flora and, as its name implies, represents the meeting ground of

elements from the more tropical north and from the specialised Cape flora to the south (22). The latter on the whole predominate, or at least do so over much of this region, and it may be regarded more particularly as related to the Cape flora. For this reason alone there would be grounds for combining the two here, but there is also an important practical reason for so doing.

The combined area of the Cape region and the transition region is roughly that of the Union of South Africa, and the flora of this political area has been analysed in great detail by Phillips (183), so that by combining the two regions a great number of statistics are conveniently to hand.

According to Phillips the flora of the Union of South Africa contains 1,500 genera with native species, and of these no fewer than 488 are endemic, giving a proportion of about 30 per cent., a figure perhaps not exceeded anywhere. The flora also includes a number of endemic families, but these are for the most part small.

As might be expected, the endemic genera vary from monotypes, of which there are about 200, to genera with over one hundred species. Among these latter are *Agathosma*, *Aspalathus* and *Heliophila*, and other large genera are *Gasteria*, *Lachenalia* and *Leucadendron*.

The endemics are specially numerous in certain families. For example *Elegia*, *Hypodiscus*, *Thamnochortus* and *Willdenowia* belong to the Restionaceae; *Lebeckia*, *Podalyria*, *Priestleya* and *Rafnia* to the Leguminosae; *Grisebachia*, *Salaxis*, *Scyphogyne*, *Simoecheilus* and *Sympieza* are closely related genera of the Ericaceae; and *Chrysocoma*, *Eriocephalus*, *Metalasia*, *Oldenburgia*, *Pteronia* and *Relhania* belong to the Compositae.

Among other endemic genera belonging to less conspicuous families are *Freesia*, *Galtonia*, *Mimetes*, *Prismatocarpus*, *Rochea*, *Roella*, *Roridula*, *Sarcocaulon* and *Strelitzia*.

It must also be remembered that many of the genera included in wider African categories are in fact almost entirely confined to this part of South Africa.

The case of *Mesembryanthemum* (Plate 11), one of the most characteristic of all South African genera, requires special comment. In its old conception of a single huge genus of several hundred species, *Mesembryanthemum*, although almost entirely confined to South Africa, was not entirely so since a handful of species extended to a considerable distance elsewhere. In recent years, however, this huge genus has been split up into about one hundred smaller genera, mostly of only a few species each. Of these practically all are confined, often very narrowly, to South Africa and have the effect of appreciably increasing the number of genera endemic to that kingdom.

Indian Region

This region is to some extent heterogeneous because it comprises not only the Indian Peninsula proper but also the island of Ceylon and the lower tropical flanks of the Himalayas.

Willis (262) gives the number of endemic genera in India and Ceylon at over 300, and about one-quarter appear to be found in both mainland and island.

About twenty-five genera are confined to Ceylon, among them being *Doona* and *Nargedia*.

A small proportion of the remainder are found along the base of the northern mountains or on the tropical part of their southern flanks, and among these are *Corallobotrys* and *Luculia*.

The rest are endemic to the Indian Peninsula proper or to Ceylon as well. The genera *Aegle*, *Chloroxylum* and *Zeylanidium* are instances of the former, while *Elettaria*, *Feronia*, *Frerea*, *Melocalamus* and *Wallichia* exemplify the latter.

Continental South-east Asiatic Region

This region comprises southern Burma, tropical South China, Formosa, Siam, Annam and the Malay Peninsula, and it is difficult to estimate the number of endemic genera, but from various compilations it appears to be well over 200. Very few of these are widespread in the sense that they occur both in the north and on the Peninsula.

Most of the endemics are, as might be expected, found in the larger northern part of the region, and these include *Oroxylum*, *Rhaphis* and *Sarcodium*.

Among genera confined to the Malay Peninsula are *Aulacodiscus* and *Maingaya*.

A small but conspicuous group of genera link this region up with the Indian. Some of them range from India to Siam, and others all the way to the Malay Peninsula, among them being *Pentasacme*, *Sapria* (Himalayas and Siam), and *Sphinctacanthus*.

Region of the Malayan Archipelago

For many reasons, and especially those connected with theories of palaeogeography, the Malayan Archipelago is one of the most interesting regions in the world.

If a map showing the depths of the sea is consulted it will be seen that the western part of the Archipelago, comprising Java, Sumatra and Borneo (or the Sunda islands as they are called), is separated from the mainland of Asia only by shallow waters with a depth of less than 600 feet. These islands are therefore generally regarded as rising from a continental shelf which is a prolongation of the Asiatic continent and which is called the Sunda shelf. Similarly in the eastern part of the Archipelago the islands of New Guinea and Aru will be seen to be joined in the same way to Australia and to be part of what is called the Sahul shelf. Between these two parts are a number of islands each separated from one another and from the groups just mentioned by much deeper water. This region, which includes the Philippines, Celebes, Timor, Ceram and the Lesser Sundas, has been termed a "zone of disquiet relief."

It is thus seen that geographically the Malayan Archipelago has three parts, a western Asiatic zone, an eastern Australian zone and an intermediate zone. It has also long been realised that the flora and fauna of the region shows a similar segregation, although this is sometimes rather obscure and many attempts have been made to draw an imaginary line marking the junction of the western and eastern biota (289).

One of the earliest and perhaps the best known of these is "Wallace's Line" which runs east of Borneo and between the small Sunda islands of Bali and Lombok. This, it will be noted, actually marks the east edge of the Sunda shelf, and was based largely on the facts of animal distribution.

The more recent line of Weber makes the chief demarcation just west of New Guinea, and therefore follows the western edge of the Sahul shelf.

It is outside our province here to discuss the merits of these lines further, but they help us to visualise what is the most important botanical feature of the region



Plate 9. Gunnera chilensis in S. Chile

(from Karsten & Schenck, Vegetationsbilder)

as a whole, namely that the flora consists of two important elements, the Asiatic and the Australian, and that the middle part of the Archipelago particularly shows a great mingling of them. It is also generally true to say that the Asiatic element is the larger and more extensive and that this predominates in the west, while the Australian element predominates, or is at least most obvious, in the east. What has been said also makes clear that any comprehensive botanical account of the region is impossible within the space available here and that it is possible only to refer to some of the leading features. The remarks that have been made must, however, be borne in mind, especially in relation to the subject matter of Chapter 20.

The number of endemic genera in the Archipelago is certainly very large, but owing to the heterogeneity of the region it is difficult to arrive at a total figure. It is probably at least 500.

A fair proportion of these, and they are the hardest to estimate, range more or less all over the islands, and these include *Althoffia*, *Dryobalanops*, *Geunsia* and *Pangium*. There is also almost every combination of two or more islands. *Clemensia*, *Philbornea* and one or two others, for instance, form a group recorded only from Borneo and the Philippines.

In addition almost every separate island, including even some of the smallest, has one or more. New Guinea can confidently be said to have most, perhaps 150, and its flora is very remarkable, though none of the genera are particularly familiar.

The Philippines and Borneo come next with perhaps 100 each, the latter including *Burbridgea*. Then comes Java, followed at some distance by Sumatra, with not more than about twenty. The remaining islands all have much smaller numbers.

The Polynesian sub-kingdom (170, 275)

The next four regions all fall within what may, in broad terms, be called "Polynesia," although this name is properly applied to one of them only. Although their floras are statistically of very different values, they are all of them, for theoretical reasons, of exceptional interest and it has been thought desirable here to give as complete a list as possible of their endemic genera. The data are, however, not easy to collect and further investigation may well make it necessary to modify some of the details given, but these particulars may at least assist those investigations, which are very much to be desired.

Two of the regions, Hawaii and New Caledonia, have rich and very remarkable floras, but those of the other two are much smaller and less specialised. Indeed, except for the first two there is really no "Polynesian flora," and what there is seems to be entirely derived.

Only fourteen genera are found in two or more of the four regions, namely:

Agatea, *Burarea*, *Crossostylis*, *Meliadelpha* and *Storckia* in New Caledonia and Polynesia proper,

Calycosia, *Chelonespermum*, *Coelococcus*, *Lepinia* and *Veitchia* in Polynesia and Micronesia,

Chiostigma in the Lord Howe Islands, the New Hebrides and Samoa,

Phyllostegia in Hawaii and the Society Islands,

Pritchardia in Hawaii and Fiji,

Reynoldsia in Hawaii, Samoa and Tahiti.

Hawaiian Region

This is one of the most isolated regions in the world and its flora shows a high degree of endemism. The two most important relationships in the flora are the Asiatic and the American, and the latter greatly predominates.

The number of endemic genera is about fifty, a proportion of some 20 per cent., and they belong to eighteen families of which one or two are specially well represented. For instance, the genera *Brighamia*, *Clermontia*, *Cyanea*, *Dellissea*, *Rollandia* and *Trematolobelia* are all woody members of the Lobeliaceae (see p. 77), while *Raillardia* is one of six Composite endemic genera.

Of the rest *Kadua*, with sixteen species, is one of the largest, and others are *Bobea*, *Hillebrandia*, *Labordea* and *Nothoecstrum*.

Region of New Caledonia

In our classification there are included here the Lord Howe Islands and Norfolk Island which would otherwise have to be treated separately. They may be dismissed at once with the statement that the former has four endemic genera, namely *Colmeiroa*, *Hedyscepe*, *Howea* and *Negria*, and the latter two, namely *Pseudomorus* and *Streblorrhiza*.

The flora of New Caledonia is of the greatest interest not only for its marked endemism but also because of its floral relationships. It contains as far as can be estimated well over one hundred endemic genera ranging over twenty-seven families.

Unfortunately, although these are of great interest, they are all of them likely to be unfamiliar, and it must suffice to mention as examples *Alphandra*, *Gongrodiscus*, *Kentiopsis*, *Pancheria*, *Pritchardiopsis* and *Strasburgeria*.

Region of Melanesia and Micronesia

Apparently only six genera are endemic to this region, namely :

<i>Bentinckia</i>	.	.	.	Bonins and Carolines.
<i>Cassidispermum</i>	.	.	.	Solomons.
<i>Gulubia</i>	.	.	.	Palau.
<i>Platypholis</i>	.	.	.	Bonins.
<i>Pseudomacodes</i>	.	.	.	Solomons.
<i>Sararanga</i>	.	.	.	Solomons.

Region of Polynesia

The total number of endemic genera here appears to be twenty-three, namely :

Acicalyptus, *Amaroria*, *Dolicholobium*, *Graeffea*, *Heteropanax*, *Leucosmia*, *Neoveitchia*, *Paphia*, *Pareugenia*, *Pelagodendron*, *Pimia*, *Richella*, *Squamellaria*, *Trimenia* and *Vitiphoenix* on Fiji.

Apetahia, *Bonnierella*, *Fitchia*, *Hitoa*, and *Sclerotheca* on the Society Islands.

Badusa on Fiji and the Society Islands.

Naudiniella on Samoa and the Society Islands.

Solfia on Samoa.

Endemic genera of Tropical America

Just as in Africa, there are in tropical America many endemic genera with ranges that transcend the limits of any one region. Some of these approach in

extent of distribution genera which elsewhere have been described as "wides," but they vary a great deal and it is more generally convenient to include them here as a special more widespread type of American endemics, and this may be justified on the grounds that their interest lies more in the fact that they are confined to tropical America than in the fact that they do not happen to be confined to one region.

This reflects to some extent on the value of the regions as defined in the floristic classification, but enough has already been said to show that these are indeed real entities. It seems rather that in the tropics of the New World, which form an extensive and homogeneous area, geographical segregation and isolation has never been very great and that, as a result, endemism is, as it were, on a rather wider scale.

The number of genera endemic in this wider sense to tropical America is certainly very large. Willis (262), for instance, has estimated that there are 1,700 South American endemic genera, and a large proportion of these will undoubtedly fall under the present heading, so it is probably safe to envisage a total of at least 500.

Their ranges vary enormously but various influences lead to the predominance of three main types. First, there are the genera which extend practically all over the whole area including Central America and the West Indies. Next, there are those confined to the western, Andine, side of the land but which extend so far north and south that they cover two or more floristic regions. Finally, there are the genera which are mostly to be found within the great area of Brazil but which extend thence varying westward or north-westward.

These groups as a whole include many large and familiar genera and especially many of the choice orchids commonly grown in hothouses in Europe. Among good examples are :

1. Genera found more or less throughout tropical America :
Caryocar, Cecropia, Cedrela, Gloxinia, Lycaste, Maranta, Monstera, Ochroma, Oncidium, Tecoma, Theobroma.
2. Genera chiefly in Brazil but extending west and north-west therefrom :
Cattleya, Cephalocereus, Jacaranda, Jacobinia, Laelia, Miltonia.
3. Genera found chiefly in western tropical America :
Cinchona, Cosmos, Mammillaria, Phytelphas.

Caribbean Region

This region consists of two well-marked areas, Central America and the West Indies, and the former has a close relationship with western North America. Owing to the absence of modern floras it is difficult to estimate the total number of endemic genera, but it is probably at least three or four hundred. *Bouvardia, Guajacum, Hura* and *Swietenia* (which is actually said to reach Peru) exemplify genera found more or less throughout the region.

Probably less than half the endemic genera are confined to Central America and particularly to Mexico, and the latter include *Dahlia, Euchlaena, Martynia* and *Polianthes*.

More than half the genera are confined to the West Indies and *Crescentia* is but one of many characteristic genera here.

Agave is a good example of a genus which extends rather beyond the strict limits of the region, being centred in Mexico but ranging to the south-western U.S.A. and to northern South America. *Furcraea* is similar but less northerly.

The Bahamas are said to have only one endemic genus, *Neobracea*, and the Bermudas have none.

Region of Venezuela and Guiana

Although there are sufficient reasons for maintaining this area as a distinct region floristically, it is not surprising that it has very close relationships with the next two, the Andine and the Brazilian, and its generic endemism appears to be small, perhaps not exceeding about fifty. In addition, few of these are either well-known or familiar plants and there need only be mentioned *Heliamphora*, *Manicaria* and *Voyria*.

Brazilian Region

This huge region has one of the richest floras in the world, but also one of the least well known. Physiographically the region is made up of two very distinct parts, the basin of the Amazon, and the uplands (catingas) and mountains to the east, and many floristic classifications reckon these as two regions. They are combined here, however, because the relevant literature is rarely detailed enough to enable a proper separation to be made, though actually but few of the endemic genera are found in both.

The number of endemics in the region as a whole is certainly very large, and judging from the total size of the flora there may be as many as a thousand. Very few of them are either large or familiar. Perhaps the best known of all are *Victoria*, containing the huge water-lily of the Amazon, and *Hevea*, which, in the Para rubber tree, affords one of the most important of all economic plants. *Arachis*, the earth-nut, is also a native of Brazil as far as can be ascertained.

Willis (263) and others record several genera found only in the neighbourhood of Rio de Janeiro, and these, which include *Congdonia*, *Fernseea*, *Itatiaea*, *Macro-dendron*, *Ramusia* and *Sphagneticola*, must rank among the most narrowly distributed of all genera.

Andine Region

Although the whole Andine region from Colombia to southern Chile is to be regarded as a single elongated region, it is convenient to consider it here as made up of two rather distinct parts, tropical and temperate, and these are fairly clearly marked politically. In the northern tropical part are the four montane countries of Colombia, Ecuador, Peru and Bolivia, while the southern part consists essentially of Chile (though it includes also the western part of Argentina) and may be referred to by this name. The Andine region as defined in our classification also includes the Galapagos Islands.

The flora of the tropical Andes is very rich and also, on account of the range of elevation, very varied. Each constituent country has many endemics, so that the total is probably several hundreds, and they are found chiefly on the tropical flanks of the mountains, the highland element in the flora having generally a wider range. Among the more familiar endemic genera are *Cochlioda*, *Desfontainia* and *Eccremocarpus*.

The flora of the Galapagos Islands (143) is of great interest from the point of view of its species but contains very few endemic genera, *Leiocarpus* and *Scalesia* being the only important ones. It is chiefly for this reason that the archipelago has not been given regional rank.

The flora of Chile has recently been analysed in some detail in connection with the flora of temperate South America as a whole (98), and from this it appears



Plate 10. Cacti with an Epiphytic Species of Bromeliaceae in Mexico

(from Karsten & Schenck, Vegetationsbilder)

that there are about 125 endemic genera, a high percentage considering the size of the flora as a whole. *Jubaea*, *Lapageria* and *Lardizabala* are noteworthy examples, the first-named being one of the few palms found outside the tropics, and others include *Berberidopsis*, *Fascicularia*, *Francoa*, *Schizanthus* and *Tecophilaea*.

Pampas Region

Strictly speaking this region comprises the great grass-steppe between the Andes on the west and the river Parana on the east, but for present purposes it may be regarded conveniently as comprising Argentina, Paraguay and Uruguay.

The endemic genera are not numerous. The analysis mentioned above shows that Argentina has about sixty-five, but none calls for special mention.

Paraguay and Uruguay have also a few endemic genera, and the total for the region may therefore be estimated at round about one hundred.

Region of Juan Fernandez

This small archipelago, which lies 400 miles off the coast of Chile, has a very remarkable flora which has been particularly studied by Skottsberg (223). It has a very high degree of endemism including about a dozen genera. Among them are *Juania*, a palm; *Lactoris*, which forms an endemic monotypic family; and one or two remarkable Composites, including *Dendroseris* and *Rhetinodendron*.

Other American endemic genera

As in tropical America there are, in temperate South America, a number of genera which, while not falling under any one region, must nevertheless be considered as endemics. These consist chiefly of genera characteristic of the temperate Andes but which extend therefrom eastward across Argentina and Patagonia for various distances.

In all there are about eighty such genera, and among them are *Azara*, *Cajophora*, *Myzodendron*, *Nassauvia* and *Triptilium*.

Australian endemic genera

The Australian continent supports one of the most peculiar as well as one of the richest of the world's floras (36). Indeed, its very degree of peculiarity, combined with its relative unfamiliarity, leads to a difficulty because it is totally so different from other floras (its only appreciable relation being with South Africa) that there is a tendency to regard it as a single unit, whereas in fact there is room for a classification as complete as that of other continents. Another complicating factor is that the flora is very uneven. It is richly developed in the east and south, and especially in the south-west, but it is less so in the middle parts of South Australia and is poor in the interior and north. There is also a great range of latitude, and the flora of northern Queensland is very different from that of the south-west or of Tasmania.

The recognition of three regions, the eastern, the south-western and the central, expresses the main segregation of the flora, but, as was the case in America and Africa, there are many genera which range much more widely although exclusively within the continent, and these must be considered first.

The total number of genera endemic to Australia is estimated at over 500, many of them, like those of South Africa, being large and markedly peculiar genera, and of these probably nearly one-half are so widely ranging that they cover all or parts of two or more of the constituent regions.

Many of these range almost all over the continent except for the dry regions of the centre and north, and among them are *Actinotus*, *Banksia* (one species has been said to reach New Guinea), *Dryandra*, *Haemodorum*, *Hakea*, *Psilotus* (100 spp.), *Pultenaea* (80 spp.), *Trachymene* and *Xanthorrhoea*.

Very many others extend more or less completely through the southern latitudes of the continent from west to east. A few like *Correa* are more characteristically eastern, but the great majority are centred in the south-west and have but a few species ranging east. Good examples of these are *Boronia* (60 spp.), *Chorizema*, *Darwinia*, *Daviesia*, *Dillwynia*, *Goodenia* (100 spp.), *Jacksonia*, *Kennedyia* and *Petrophila*.

North and East Australian Region

This is an unsatisfactory region because of the enormous latitudinal range it embodies, and it is only to be expected that the flora of northern Queensland, which lies within the tropics, will be very different from that of Tasmania, which lies beyond 40° S.

It appears to contain about 150 endemic genera in all, and few of them range throughout it. Most of them are confined to Queensland and are exemplified by *Carnarvonia*, *Darlingia* and *Newcastlea*. At the other extreme Tasmania has a few endemic genera, including *Bellendenia* and *Milligania*.

The remainder are chiefly in the south-eastern regions of New South Wales and Victoria and in South Australia, and include *Brunonia*, *Callicoma*, *Humea* and *Telopea*.

South-west Australian Region (295)

This region stands out among the Australian regions in the richness of its flora and in its high degree of endemism, and it is, indeed, perhaps the only flora which compares (as it does in this and many other ways) with that of the Cape Region of South Africa. Both, it will be noted, occupy the extreme corner of a huge continental mass.

Its endemic genera, however, do not give a real picture of its peculiarity, because some of the most characteristic genera actually range far outside it and have already been mentioned, and this peculiarity will be plainer when the species are discussed.

The number of more or less strictly endemic genera seems to be in the neighbourhood of one hundred, and by the nature of the case they are all very local. *Cephalotus*, for instance, which forms a monotypic family, occurs only in one small river valley. Others rather more widely distributed are *Anigozanthos*, *Byblis*, *Dasyopogon*, *Eremaea*, *Kingia* and *Loxocarya*.

Central Australian Region

This region needs but little notice here, not only because the number of endemics is small but also because it is still imperfectly known. The endemic genera probably do not exceed thirty, and it must suffice to say that they include *Austrobassia*, *Dimorphocome* and several small Cruciferous genera.

New Zealand Region

For a number of reasons the flora of New Zealand is of special interest to the plant geographer, and it has been so much studied that its constitution is now well known (70). It will receive more adequate attention under the heading of species, but it may be said here that the number of endemic genera is about thirty. Most of these are fairly well distributed, but a few are very restricted, the most marked of these being *Coxella* and *Myosotidium*, which are found only on the Chatham Islands.

Other endemics, mostly monotypes, are *Corokia*, *Haastia*, *Hoheria*, *Phormium* and *Stilbocarpa*.

The Kermadec Islands, which also belong to this region, have no endemic genera.

Patagonian Region

This region, which may be described as comprising the lowland parts of extreme southern America, has a small flora and practically no endemic genera. Some of those already mentioned for Chile and Argentina perhaps actually fall mostly within this region, but as they have already been mentioned they need not be considered again. The most isolated part of the region, the Falkland Islands, has no endemic genera at all.

Region of the South Temperate Oceanic Islands

The flora of this region is extremely small, but it is of exceptional interest for many reasons and will receive detailed treatment later. There are only two endemic genera in it, namely *Lyallia* on Kerguelen and *Pringlea*, whose distribution, owing to the configuration of the region, is discontinuous and which has already been mentioned under that heading.

The Proportion of Endemic Genera in the two Hemispheres

This lengthy account of endemic genera may fitly be concluded by an attempt to estimate the number of such genera in each of the two hemispheres, northern and southern. It is not altogether easy to make this computation, because several regions lie across the equator, but if some arbitrary proportionment of these is adopted it appears that there are about twice as many endemic genera in the southern hemisphere as there are in the north. This is using the term endemic as it has been defined for the particular purposes of this chapter. If it is made more narrow in conception, then the disparity in numbers is certainly accentuated, and of extremely restricted genera the great majority are undoubtedly southern.

These bare figures are sufficiently noteworthy, but the position can only be appreciated properly if the relative areas of land in the two hemispheres are taken into account. It was seen in Chapter 2 that the land area open to plant habitation in the north is about 38 million square miles, while in the south it is only 13 million, a proportion of nearly three to one, and it would appear therefore that the density or frequency of endemic genera is six times as great in the south as in the north.

CHAPTER 8

THE DISTRIBUTION OF SPECIES—I

THE number of families of Flowering Plants is such that it was possible, in Chapter 4, to mention them individually.

The number of genera is so much greater that even in three chapters only a few of them could be mentioned ; but it was possible to make a complete statistical analysis of them.

The number of species is so huge that even this is impossible and only a very generalised survey can be attempted. The problem is what to include and what to omit.

Whatever else may be desirable, the essential purpose of this survey must be to demonstrate what is certainly the most important feature in the distribution of species, namely that these are representatives of every kind of range that the geography of the world permits. The illustration of this leading fact may be taken as the general theme of this and the next three chapters.

That many genera consist of only one species, and that the ranges of others are but the sums of the ranges of their constituent species, are enough indication that there is no real difference between the distribution of species and the distribution of genera, except, of course, that the latter is generally more extensive.

This being so, much the same arrangement of treatment can be adopted with regard to species as was employed in the case of genera, and if this framework is supplemented by special reference to certain particularly important aspects of species distribution, the main purpose mentioned above can be sufficiently achieved.

The subject matter of the four chapters describing the distribution of species therefore begins with a discussion of species numbers in general. This is followed by a description of the distribution of species in a few selected large genera. Wide species are dealt with next. Then comes a survey of endemic species, arranged, as far as is appropriate, according to the thirty-six floristic regions, and finally certain particular aspects of species distribution receive special attention.

Number of Species

There are various estimates of the total number of species of Flowering Plants, but there is none both detailed and up to date, and it is only possible to compute the numbers roughly.

One of the most detailed estimates is that published by Thonner in connection with his study of the flora of Africa, and this can usefully be used as a basis for consideration here. Thonner (246) puts the total number of species in the whole world at 136,000, of which 24,500 are Monocotyledons and 111,500 are Dicotyledons, and the number of genera as about 10,000, giving an average of 13.6 species per genus. This last figure accords pretty well with other estimates of genus size and helps considerably towards a more modern total computation. There is reason to believe, as has already been said, that the total number of genera is to-day somewhere between 12,500 and 15,000, and if, as may be provisionally assumed, the average size of these is that given by Thonner, then it would appear that the total

number of species is somewhere between 170,000 and 200,000. This, of course, includes only species which have been described, and many certainly remain to be discovered. These latter cannot be enumerated but, bearing in mind how very completely the flora of the world is known to-day, they cannot be proportionately very great. All that can be said is that the total number of existing species probably does not exceed 200,000 and may be somewhat less.

More interesting than the rather bald total figure are those which have been given from time to time regarding the species population of different parts of the world's surface. Such figures have recently been employed by several writers in attempts to assist in the recognition of natural floristic regions and also for the purpose of estimating the value of floras on a basis of species concentration. Wulff (270, 292), for instance, has published a long list of such figures, and Szymkiewicz (237), Taylor (241) and, to a lesser degree, Marie Victorin (158) have also contributed statistics. They are, however, mostly taken from such sources, like local Floras, as happen to be available, and therefore vary a good deal in date and value. On the other hand many of them are quite up to date.

As it is interesting to have these figures in tabulated form, many of them are given below under the different floristic regions to which they refer. It will be necessary in some cases to repeat them later. Only reasonably modern estimates are included. Unfortunately they do not always indicate whether they refer only to indigenous species or to both natives and adventives, but for the most part the latter may be assumed. Only in the case of certain very small regions like some oceanic islands is the difference between total species and native species very considerable, and where necessary this will be referred to later. The figures have for the most part been rounded off to the next higher hundred, and have been arranged according to the various floristic regions.

Collected estimates of the number of species in various floras

Arctic and Sub-arctic Region :

Arctic North America, 450 ; Arctic North American Archipelago, 200 ; Ellesmere Land, 108 ; Franz Joseph Land, 137 ; Greenland, 390 ; Novaia Zemlya, 200.

Euro-Siberian Region :

Caucasus, 5,700 ; Denmark, 1,600 ; France, 3,900 ; Germany, 2,680 ; Iceland, 375 ; Kamchatka, 800 ; Kuriles, 768 ; Norway, 1,350 ; Poland, 2,000 ; Sakhalin, 300 ; Switzerland, 2,600.

Sino-Japanese Region :

China, c. 20,000 ; Japan, 5,800 ; Korea, 2,165.

Western and Central Asiatic Region :

Tibet, 700 ; Tibetan Plateau, 741.

Mediterranean Region :

Balearics, 1,280 ; Balkan Peninsula, 6,530 ; Corsica, 1,590 ; Crete, 1,500 ; Cyprus, 1,170 ; Italy, 3,900 ; Malta, 716 ; Palestine, 2,200 ; Sardinia, 1,534 ; Sicily, 1,800 ; Spain, 4,500 ; Syria, 2,865.

Macaronesian Transition Region :

Azores, 600 ; Canaries, 1,550 ; Cape Verdes, 400 ; Maderia, 686.

Atlantic North American Region :

Canada as a whole, 6,000 ; Central North America, 4,000 ; Central and North-east U.S.A., 4,900 ; Newfoundland, 900 ; Quebec, 3,000 ; South-east U.S.A., 6,700.

Pacific North American Region :

Alberta, 2,300 ; California, 4,000 ; Colorado, 3,000 ; Nevada, Utah, etc., 3,600 ; New Mexico, 3,000 ; North-west U.S.A., 3,000 ; Rockies, 5,900 ; South-west U.S.A., 3,000.

North African—Indian Desert Region :

Arabia, 2,144 ; Central Sahara, 300 ; Cyrenaica, 1,500 ; Egypt, 1,500.

Sudanese Park Steppe Region :

Sudan, 2,700.

North-east African Highland and Steppe Region :

Italian Somaliland, 600 ; Socotra, 600.

West African Rain-forest Region :

Tropical Africa as a whole, 13,000 ; Congo, 3,000.

South African Transition Region :

Union of South Africa as a whole, 15,000.

East African Island Region :

Aldabra, 71 ; Madagascar, 5,500 ; Mauritius, 900 ; Réunion, 300 ; Rodriguez, 200 ; Seychelles, 350.

Indian Region :

Ceylon, 3,100 ; India, c. 21,000.

Continental South-east Asiatic Region :

Formosa, 3,700 ; Hong Kong, 728 ; Malay Peninsula, 7,000.

Region of the Malayan Archipelago :

Malaya as a whole, including the Peninsula, c. 20,000 ; Borneo, 11,000 ; Java, 5,000 ; New Guinea, 6,872 (74 of its families only) ; Philippines, 10,000.

Hawaiian Region :

Hawaiian Islands, 1,000.

Region of New Caledonia :

Lord Howe Island, 160 ; New Caledonia, c. 3,000.

Region of Melanesia and Micronesia :

Bismarck Archipelago, 700 ; Caroline and Palau Islands, 450 ; New Hebrides, 570.

Region of Polynesia :

Easter Island, 32 ; Fiji, 1,100 ; French Polynesia, 600 ; Samoa, 548 ; Tonga Island, 257.

Caribbean Region :

Bahamas, 1,000 ; Bermudas, 165 ; Cedros Island, 135 ; Cuba, 7,000 ; Central America, c. 12,000 ; Porto Rico, 3,800 ; St. Vincent, 850 ; West Indies, 3,000.

Region of Venezuela and Guiana :

Venezuela, 6,800.

Brazilian Region :

Brazil as a whole, c. 40,000.

Andine Region :

Chile, 5,500 ; Galapagos Islands, 332.

Pampas Region :

Paraguay, 4,220 ; Uruguay, 2,250.

Region of Juan Fernandez :

As a whole, 142.

Cape Region :

Includes over 800 Leguminosae ; Cape Peninsula, 2,500.

North and East Australian Region :

Australia as a whole, c. 12,000, including 1,200 Leguminosae ; New South Wales, 3,800 ; Queensland, 4,400 ; Tasmania, 1,127 ; Victoria, 2,200.

South-west Australian Region :

Western Australia, 4,400.

New Zealand Region :

Auckland Islands, 189 ; Campbell Island, 115 ; Kermadecs, 161 ; New Zealand, 1,843.

Patagonian Region :

Falkland Islands, 176 ; Fuegia, 615 ; Magellansland, 330.

Region of the South Temperate Oceanic Islands :

As a whole, c. 80.

Distribution of Species within Genera

Genera vary enormously in the relative distribution of their constituent species, and even those which are alike in total range are often quite dissimilar when the actual distribution of their species is taken into account. In some genera there is a fairly high proportion of wide species ; in others the species are practically, and in some cases entirely, endemics. In the former the wides may be of comparable range and fairly evenly scattered, or there may be one or more which exceed the rest and which may even attain the whole area of the genus. In the latter endemics may be found in all parts of the genus area, or they may be massed in one part of it. Some genera illustrate several of these features to some degree.

In order to illustrate these and other more detailed points eight large genera have been selected and the detailed distribution of their species is here described. They have been chosen as covering between them most of the world and most aspects of interest in the geography of species. Two, *Plantago* and *Juncus*, are almost world-wide, but chiefly temperate, genera ; two, *Begonia* and *Dioscorea*, are almost pan-tropical ; *Drosera* is predominantly a southern genus ; *Viola* is a widespread but discontinuous temperate genus ; and *Rhododendron* and *Erica* have each great numbers of endemic species in one particular region.

The distribution of the species of Plantago

The genus *Plantago*, which has been revised by Pilger (69), has about 250 species and is a good example of a genus which is actually found, owing to the cosmopolitan range of one or two widely introduced species, almost all over the world, but which is essentially temperate in its natural distribution.

The total range is almost world-wide except that in many parts of the tropics the genus is represented only by the adventive species, *P. major* and *P. lanceolata*, and even these are absent from the low-lying parts of tropical America.

About twenty species can be said to have a wide range, and of these the only marked examples are *P. media* in Eurasia, *P. asiatica* from the Himalayas to

Java, *P. macrocarpa* from Kamchatka to north-western America, *P. erosa* from Ceylon to western China, *P. depressa* in Central and eastern Asia, *P. hirtella* from Mexico to Uruguay and *P. triantha* in Australia and New Zealand.

Nine species have widely discontinuous ranges, namely, *P. maritima*, northern hemisphere and Patagonia; *P. Durvillei*, California and the tropical Andes; *P. heterophylla*, North America, Uruguay and Paraguay; *P. trimenta*, Chile and Juan Fernandez; *P. crassifolia*, Mediterranean and South Africa; *P. canescens*, eastern Siberia and north-west America; *P. amplexicaulis*, Canaries and Mediterranean; *P. ovata*, Canaries and western and central Asia; and *P. lanigera*, New Zealand and, recently, New Guinea.

This leaves over 200 species of what may be called endemics, that is to say, species more or less rigidly confined to one region. The distribution is as follows:

Western North America	5
Eastern North America	15
Mexico	5
Western tropical South America	39
Temperate South America	42
Europe, Mediterranean and west Asia	42
Central Asia	10
East Asia	10
Formosa	2
Java	2
Madeira and Canaries	4
Tropical African Mountains	2
South Africa	4
Madagascar	1
Australia	16
New Zealand	4
Hawaii	9

together with the following very narrowly distributed species:

<i>P. fernandezia</i>	Masa Tierra.
<i>P. Hedleyi</i>	Lord Howe Island.
<i>P. robusta</i>	St. Helena.
<i>P. rupicola</i>	Rapa Island.
<i>P. rapensis</i>	Rapa Island.
<i>P. aucklandica</i>	Auckland Island.
<i>P. picta</i>	E. Cape Island, New Zealand.
<i>P. pentasperma</i>	Amsterdam Island.
<i>P. Stauntoni</i>	St. Paul Island.

The distribution of the species of Juncus

In contrast to *Plantago*, *Juncus* has very few species which are anywhere adventive. As revised by Vierhapper (73), the genus has about 225 species, and of these something between one-third and one-half are wides—a very high proportion.

The widest of all is *J. bufonius*, which is almost cosmopolitan. It is worth noting that this is the only member of the genus which is a common weed of cultivated land and its great range may be to some extent adventive. This latter is true also of certain other species such as *J. tenuis*, which is widespread in America and introduced here and there in the Old World; *J. capitatus*, which occurs

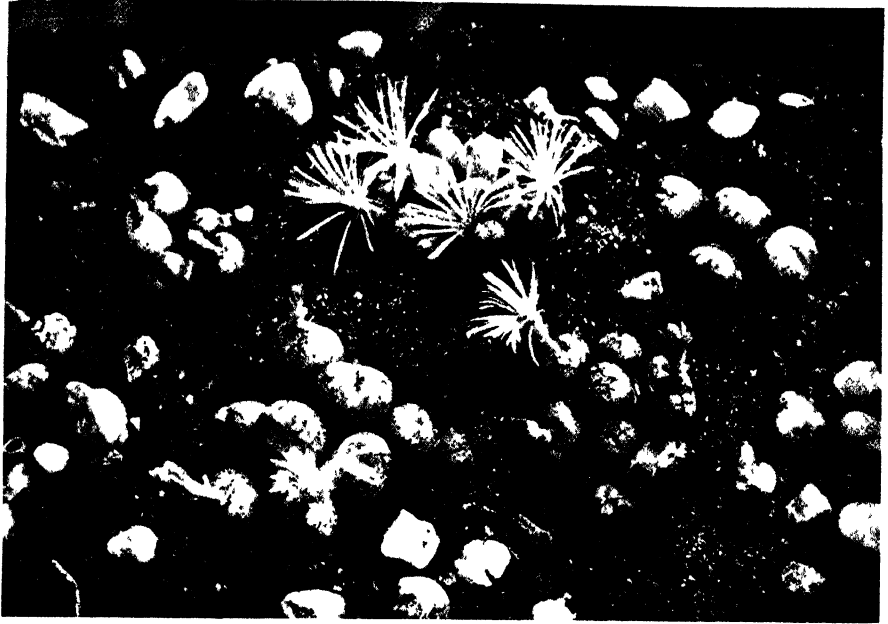


Plate 11. Stone-like Species of Mesembryanthemum

(from Graebner, Lehrbuch der Allgemeinen Pflanzengeographie)

naturally in Newfoundland, Europe and Africa, and which is introduced into Australia; and the Eurasian *J. inflexus*, which is introduced in South Africa and New Zealand. *J. articulatus* and *J. bulbosus* are both characteristic of the temperate parts of the Old World but have a limited distribution in North America.

Other wides include a conspicuous group of arctic-alpine species with a more or less circumpolar range and which occur also in some or all of the north temperate mountains, among them being *J. triglumis* and *J. biglumis*.

Among more temperate northern species are *J. conglomeratus* and *J. Gerardii*, and on a narrower scale *J. compressus*.

Several species range more or less continuously from North to South America as, for instance, *J. dichotomus*, *J. andicola* (from Alaska to Patagonia), and *J. marginatus*. Similarly in the eastern part of the Old World there is a link between the north and south by *J. pauciflorus* from east Asia to Australasia and the Pacific Islands, and *J. prismatocarpus* from east Asia to New Zealand.

Discontinuity of range is well illustrated, and if the status of the plants is to be relied upon in all cases there are some remarkable examples. *Juncus maritimus* ranges over Europe and part of Africa and occurs again in Australia and New Zealand; *J. acutus* is in Europe, Macaronesia and the Mediterranean, and at the Cape as well as possibly on Juan Fernandez. The well-known east Asiatic-North American discontinuity is illustrated by *J. xiphioides*, while *J. falcatus* exemplifies both this and north-south discontinuity, being recorded from west North America, Japan and also from Australia. Finally, *J. planifolius* occurs in New Zealand, Australia and Tasmania, and again in South America and Juan Fernandez.

Among the remaining wides which are too numerous to be mentioned in detail all sorts of ranges are represented, as, for instance, Australia and New Zealand, both western and eastern North America, and south and tropical Africa.

Actually the most outstanding instance of the last should perhaps be included among discontinuous species. It is *J. lomatophyllus* which is said to be native in South Africa, south-eastern tropical Africa and in St. Helena.

As regards the endemic species of the genus, these again are spread over nearly the whole world, but three groups stand out. These are some forty species in either western or eastern North America, about thirty in the Sino-Himalayan mountain mass, and about a dozen in Europe or the Mediterranean.

The distribution of the species of Begonia

The huge tropical genus *Begonia* has very few wides, and the vast majority of the species are quite narrowly endemic. Indeed, according to Irmischer's revision of the genus (73), only three species merit the term wide at all, and even these are little more than endemic. They are *B. scandens* found in Jamaica, Guatemala, Guiana, Venezuela and Peru, *B. Evansiana*, which reaches from Java to North China and Japan, and *B. mollis*, which is described as widely spread on the larger Sunda Islands.

The segregation of the species over the tropics is also very marked, so that it is possible to divide the genus, without violence to its taxonomy, into four sections containing respectively African species, Asiatic species, American species, and Asiatic or American species. In other words, the main groups within the genus are confined to the continents as indicated.

In the African section species range varies from that of *B. oxyloba*, which is

found in both west and east tropical Africa, to *B. asplenifolia*, which occurs only on the top of one mountain in Gaboon. There are several species in Madagascar, but all are endemic there. Incidentally five very closely related species form a most interesting geographical series in this part of the world. They are *B. oxyloba*, already mentioned as fairly wide in tropical Africa, *B. Meyer-johannis* in eastern tropical Africa, *B. cladocarpa* in Madagascar, *B. salaziensis* in Mauritius, and finally *B. comorensis* in the Comoro Islands.

This section includes also several exceptionally narrowly distributed species, as, for instance, *B. prismatocarpa* on Fernando Po, *B. Thomeana* on the nearby island of St. Thomas, *B. perpusilla* on the island of Nossi Bé off Madagascar, *B. diptera* on the Comoro island of Johanna, and *B. annobonensis* on the west African island of Annobon.

In Asia endemic species are, as the following list of examples shows, to be found in almost every part of the area. *B. Roxburghii* is on the Himalayan-Burmese mountains, *B. malabarica* in India and Ceylon, *B. Handelii* in China, *B. tricuspidata* in Burma, *B. pseudolateralis* in the Philippines, *B. conophylla* in Sumatra, *B. Burbidgei* in Borneo, *B. renifolia* in Celebes, and *B. hirsuticaulis* in New Guinea.

Similarly in the American species, which are more numerous than the others, there are species in every region, as, for instance, *B. Franconis* in Mexico, *B. carpinifolia* in Costa Rica, *B. foliosa* in Colombia, *B. ferruginea* in Colombia and Ecuador, *B. maurandiae* in the northern Andes, *B. microphylla* in Venezuela, *B. boliviensis* in Bolivia, *B. columnaris* in Peru, *B. sanguinea* in Brazil, *B. arborescens* in the neighbourhood of Rio, *B. Fiebrigii* in Paraguay, and *B. micrantha* in Argentina.

The distribution of the species of Dioscorea

The great tropical genus *Dioscorea*, which contains the yams, has been revised by Knuth (73), who estimates that it comprises between six and seven hundred species.

Although it is found throughout the warmer parts of the world, the wide species are very few and in fact there is only one species which can claim even to approach the range of the whole genus. This is *D. bulbifera*, which occurs throughout the tropics, but it is one of the cultivated species and its natural range can now hardly be estimated. The last remark also applies to *D. esculenta*, which is described as ranging from India to the Pacific Islands. Among other wide Asiatic species are *D. glabra* from India to Java (a very common type of distribution) and *D. cirrhosa* from Hong Kong and the Liu Kiu Islands to the Philippines and Ceram (a much rarer type). Other Asiatic species include *D. nipponica* from Manchuria, China and Japan, an unusually northern range, *D. Collettii* of Burma, South China and Formosa, and the equatorial *D. polyclades*, *D. polifolia* and *D. nummularia*. Endemic Asiatic species are found in Japan, in the Philippines and in India. Very few species either reach Australia or are endemic therein.

The Asiatic species are connected with those of Africa by *D. triphylla* which ranges discontinuously over the tropics of both continents, but the total African representation is very slight and much of it actually consists of Madagascan species. Apparently none occurs on both continent and island. *D. Quartiniiana* and one or two others are widespread in tropical Africa, and there are species in the west, in the east, in the south-east, and even in South Africa proper, where they include the well-known *D. elephantipes*. *D. lanata* occurs on Socotra.

Mention of the last introduces two species which, geographically, are among the most remarkable of all. These are *D. caucasica* in the Caucasus and *D. balcanica* in Albania. Their nearest neighbour is the Socotran species just mentioned, and their curiously isolated northern range is generally considered to mean that they are relics of a more subtropical flora, most of which has now disappeared.

The remainder of the species are American and these are very numerous. Few of them are widespread even in tropical America, but there are endemics in almost every country and many ranging over two or more. They are most plentiful in South America, and here they are found both on the west and on the east. The following, selected at random, will suffice as illustrations: *D. adenocarpa* in Brazil and Paraguay; *D. campestris* in Brazil and Argentina; *D. pilosiuscula* in the West Indies and Guiana; *D. altissima* in Brazil, Guadeloupe and Tobago; *D. convolvulacea* through much of Central America and in Trinidad; *D. glandulosa* in Colombia and Argentina; *D. megalantha* in Venezuela, Colombia and Peru; *D. amazonum* in Venezuela, Guiana and Brazil; and *D. occidentalis* in the West Indies and Brazil.

The distribution of the species of the genus Drosera

(Fig. 16)

The genus *Drosera*, which contains the sundews, has been much studied by Diels (73) and others.

Only five species out of about ninety have what can reasonably be called wide ranges. The widest of all appears to be *D. indica*, which is found in tropical Africa and again from India and China to Australia. It is thus not only very widespread but also markedly discontinuous. The remaining wides fall into two groups, the first of two species, *D. rotundifolia* and *D. anglica* throughout the northern temperate zone, the latter being slightly more widespread and, incidentally, discontinuous, by its additional occurrence in Hawaii; the second of three species (among them *D. Burmanni*), which range in general from India and Japan to Australia and thus connect the northern hemisphere species with those of the south.

D. madagascariensis, which covers almost all tropical Africa as well as Madagascar, is probably the next widest species, and *D. Burkeana* has a similar range but is less wide on the continent. Narrower African species are *D. natalensis* in south-east Africa and a group of local species exemplified by *D. capensis* in the south-west Cape region. There are no purely Madagascan species.

D. intermedia, found in eastern North America and western Europe, is another markedly discontinuous species, as also, in lesser degree, are *D. brevifolia* in south-eastern North America and southern Brazil and *D. capillaris* from Texas to Guiana, the latter being the only connections between northern and southern species in the New World.

Other American species are, with the exception of *D. filiformis* in eastern North America, all southern, the widest here being *D. sessilifolia* in Guiana and Brazil; but most of them are Brazilian only, as, for instance, *D. montana*. Finally, one species, *D. uniflora*, is restricted to that part of the southern continent south of latitude 40°, and this is of special interest because the only two close relatives of this species, namely *D. Arcturi* and *D. stenopetala*, are confined to Australasia, the former being found in south-eastern Australia and New Zealand and the latter only on the New Zealand mountains.

All the other species of the genus are confined to Australasia and it is here that its great specific wealth lies. Upwards of half the total species of the genus are confined to a comparatively small part of south-western Australia, and are exemplified by *D. gigantea* and *D. myriantha*, but others range widely over the continent, as, for instance, *D. glanduligera*, on both coasts of southern Australia. There are one or two species in south-east Australia and a group, including *D. Banksii* and *D. Adelsae*, in north Australia and Queensland.

D. petiolaris is found in north Australia and in New Guinea, while *D. pygmaea* and two others (in addition to *D. Arcturi* mentioned above) connect Australia with New Zealand. Finally, there is one endemic species in New Caledonia.

The distribution of the species of the genus Viola

Turning now to pan-temperate and therefore more or less discontinuous genera, *Viola* is of much interest. In total its range is almost cosmopolitan, but its tropical representatives are mostly montane and the genus can be considered as essentially temperate. It has been monographed and revised by Becker (73).

The main feature of the distribution of the species is the comparatively large number of wides and the absence of any very marked massing of the endemic species, a contrast to what has been described for *Begonia* and *Dioscorea*. Moreover, the wides are of various ranges and not, as is often the case, restricted to the northern temperate zone, where in general widespread species tend to be plentiful.

It is true that many of the more widely spread species belong to this area, as, for instance, *V. palustris* and *V. Selkirkii* (which is more or less completely circum-polar), *V. mirabilis*, *V. canina*, *V. pinnata* and *V. collina*, which are found throughout Europe and Asia, *V. odorata* and *V. hirta*, which occur over much of Eurasia, and various species, including *V. occidentalis* and *V. incognita*, which are widespread in North America; but there are many other types of wide distribution as well.

V. Reichenbachiana and *V. Riviniana* occur in Europe and west Asia and also in Macaronesia, *V. blanda* and *V. Langsdorffii* are found on both sides of the Bering Strait, *V. altaica* and *V. dacica* range from south Europe far into Central Asia, and *V. tricolor* (in the wider sense) ranges throughout Eurasia and occurs also on the Canaries.

In lower latitudes *V. betonicifolia* has one of the widest ranges, extending more or less continuously from Afghanistan, China and Japan to Australia, including Tasmania. With similar but rather less wide ranges are *V. serpens* from Afghanistan to the Malayan Archipelago, *V. diffusa* from India and Japan to the Philippines, and *V. arcuata* from India to Java and the Philippines. *V. etbaica* ranges from Nubia to the north-western borders of India.

In the New World *V. lanceolata*, from Canada to Texas and also in Venezuela, is one of the widest, and others are *V. stipularis* in Central America, the West Indies and northern South America, and *V. scandens* from Mexico to Ecuador.

As has been said, endemic species are found in all parts of the generic range, but they are most plentiful in Europe and in the Mediterranean region. Some of these have a very narrow range indeed, as, for instance, *V. magellensis* in the Abruzzi, *V. fragrans* in Crete, *V. albanica* in Albania, *V. splendida* in south Italy and *V. athis* on Mount Athos. *V. Bertolonii* inhabits Corsica and Sardinia.

* Three noteworthy species in Macaronesia are *V. paradoxa* in Madeira, *V. cheiranthifolia* on the Peak of Teneriffe and *V. palmensis* on the island of Palma in the Canaries.

The genus is least represented in Africa, where it appears to be absent from the tropics except for *V. somalensis* in Somaliland and *V. etbaica*. In the south there are two species, *V. decumbens* and *V. sentiformis*, at the Cape.

Temperate Asia, and especially China and Japan, are fairly well stocked with endemics and include several in the Himalayas, such as *V. kashmiriana* and *V. Forrestiana*.

Endemics are also to be found, although in small numbers, over tropical Asia, as, for instance, *V. celebica* in Celebes, *V. javanica* in Java, *V. ovalifolia* in Sumatra, and *V. lunata* in New Guinea. There are at least two species in Australia and three in New Zealand, one of these also on the Chatham Islands.

In the New World there are endemic species throughout the continent. In the north some are confined to the west (e.g. *V. sarmentosa*) and some to the east (e.g. *V. pedata*), and there are several in Central America and the West Indies (e.g. *V. jalapensis* in Mexico and *V. domingensis* on Hayti).

South America, and especially the southern parts, is rich in species and compares with Europe in this respect. Most of the more equatorial species like *V. Humboldtii* and *V. arguta* are found on the Andes, but there are also several species in Brazil. Further south several small groups of species inhabit the Chilean Andes, including *V. pumila* and *V. rubella*, while others are found in the Argentine and Patagonian Andes. Finally, there are several species in Fuegia and Magellansland, an outstanding example being *V. maculata*, which is also in south Chile and the Falklands and should perhaps be considered a wide.

Discontinuous species are very few, but there is one outstanding example, *V. rostrata*, which is found in eastern North America and in Japan.

The distribution of the species of the genus Rhododendron

(Fig. 45)

Rhododendron affords a good example of the massing of endemic species in certain areas and the relative absence of wides. Many new species have been described recently, and there is no complete modern revision of the genus, but the main outline of its distribution can be gained from the *Index Kewensis* (131) and certain other sources (167).

The genus is distributed throughout the northern temperate regions with a very marked single extension south and south-east through tropical Asia to the northern part of Australia, and close on 1,100 species have been described. It is probable that if the genus is ever revised completely this number will suffer some reduction, but, on the other hand, new species are still being found, so that the figure may not be much too large.

Of this huge number no less than two-thirds, that is to say over 700 species, are found only in the great Sino-Himalayan mountain system, and of these the great majority are in that part of it where India, Burma, Tibet and China meet—the country of the great river gorges.

From this amazingly highly populated centre the genus has extensions in three directions. Much the strongest of these is through India and Malaya, and this accounts for another 200 species, divided up as follows: India and Lower Burma, 6; Indo-China and Siam, 19; Malay Peninsula, 13; Sumatra, 11; Java, 7; Borneo,

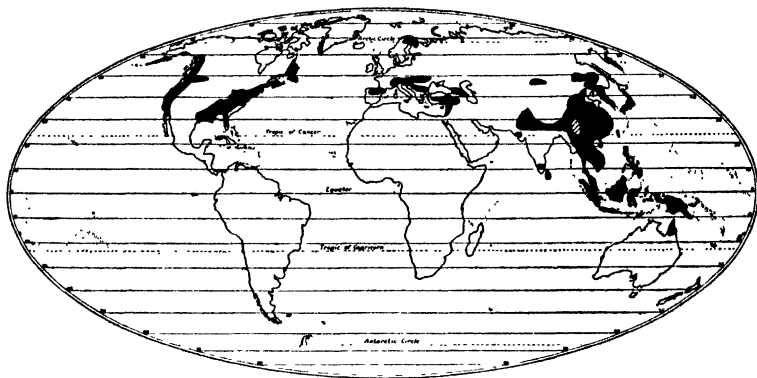


FIG. 45.—Map showing (black) the distribution of the genus *Rhododendron*, after Meinertzhagen. The small shaded ellipse in south-east Asia is the area of greatest species concentration.

29; Philippines, 24; Celebes, 3; Moluccas, 8; and New Guinea about 100. *R. retusum* is recorded from Java and Sumatra; two species have been described from the Solomon Islands; and one species, *R. Lochae*, is found in Australia.

The second extension of the genus is eastwards through eastern and north-eastern Asia, including Formosa, into and right across the North American continent. This branch of the genus comprises about 120 species distributed as follows: north-eastern Asia, 33; Formosa, 24; Japan, 45; North America, 23. *R. Anthopogon* is described as occurring in north Asia and in the Himalayas.

The third and much the smallest branch of the genus is westwards across western Asia and south Europe to Portugal. It consists of only about half a dozen species, but these include three of the best-known, namely, *R. ponticum* of the eastern Mediterranean region, which is the species of longest and most familiar horticultural history, and *R. ferrugineum* and *R. hirsutum*, the well-known "alpen-rosen" of the European mountains. *R. lapponicum* has a circumpolar arctic range.

From this summary it will be seen that out of 1,100 species only two, or possibly three, are wide in the sense that they extend beyond the limits of one floristic region. Even these are very narrowly distributed compared with the range of the genus as a whole. This, in conjunction with the fact that over 700 species are confined to what is floristically but a sub-region, gives the genus *Rhododendron* a degree of specific endemism and local concentration which is probably unique in one of its size and range.

The distribution of the species of the genus Erica

It is appropriate to pass from *Rhododendron* to a genus which can claim to compare closely with it in the features which have just been emphasised. This is the genus *Erica*, containing the "heaths." As in *Rhododendron*, there is no complete modern monograph, but the situation is here rather better because one or two publications, notably that of Phillips (183), provide useful information about the South African species, while the tropical African species have also been studied (42). Together with the *Index Kewensis* these sources provide a fairly clear picture of the distribution of the genus.

About 700 species have been described, and of these well over 600 are confined to the Union of South Africa, while of these again all but a handful are found only in the very much smaller Cape region.

From this marked geographical terminus the genus ranges in one direction only, up the east side of Africa, across the Mediterranean, and into Europe. This great south-north area is, however, in striking contrast to that of the tiny southern headquarters of the genus, comparatively poor in species, and such as there are fall into two well-marked distributional groups.

Ranging through tropical Africa from Rhodesia in the south to Abyssinia in the north, and to all intents and purposes confined to the mountains of the eastern side of the continent, are some sixteen species. All but one of these are more or less narrowly endemic, and they are more plentiful in the south than in the north. The single exception is the well-known tree heath, *Erica arborea*, which is distributed northward from tropical Africa well into the Mediterranean region and in Macaronesia. This, the only wide species in the whole genus, connects the tropical African species with the remaining group of European and Mediterranean species, which number about twenty. They include one outlier, *E. azorica*, found only on the Azores; the three species, *E. ciliaris*, *E. mediterranea* and *E. vagans*, which find their northern limits in the British Isles; and *E. Tetralix* and *E. cinerea*, which provide, in northern Europe, the northernmost records of the genus.

With only one wide species the proportion of endemics in *Erica* is even higher than in *Rhododendron*, but the latter is the wider genus and its great species centre is in the middle rather than at the edge of a continent. Moreover, *Erica* has but one centre, while *Rhododendron* has subsidiary centres in several parts of Malaya, notably in New Guinea.

The Significance of High Species Concentrations

The last two genera mentioned were selected to illustrate a common feature of distribution, the concentration of great numbers of species in one part of the generic range, and in so doing they inevitably raise the question as to whether these places of maximum species concentration can be regarded as the original homes of the genera concerned or not. In short, is it justifiable, on the strength of the species distribution, to regard *Erica* as having originated in South Africa and *Rhododendron* in the Himalayas?

Actually the two cases are rather different. In *Rhododendron* the marked partial discontinuity and the known glacial history of much of the northern temperate flora goes far to resolve the problem, and it will simplify matters if on these accounts this genus is dismissed with the remark that it would indeed be rash to maintain, merely on the basis of the present distribution of the genus, that it originated in the Himalayas.

Erica is much more difficult, and, as it is but one of a considerable number of genera with rather similar ranges, it calls for more detailed treatment here.

A steep downward gradient of species concentration away from a maximum, especially when that maximum is situated at the very extremity of a great continental mass, gives, when expressed on a map, an overwhelming first impression of migration away from the peak and in the direction of the widest land areas, this impression no doubt partly arising from the circumstance that where the scattering of inanimate objects is concerned this is the usual figure produced.

Moreover, the impression is strengthened, and can to some extent be rationalised, by an appeal to the conceptions of evolution. If, as is believed, species are produced one after another over a long period of time, it would seem that the greater the concentration of species anywhere the longer has the genus existed there.

When they are put into print it is quickly clear that both these arguments, if they can so be called, are false. The first is obviously unjustifiable, simply because a genus is not inanimate and there is no reason to suppose that living species are disposed in the way indicated. The second is unsound, because the assumption in it is based on the supposition that the rate of species production is always and everywhere the same, whereas in fact there is every evidence to the contrary.

The question of the significance of high species concentrations is but one aspect of the much wider problem of how far and by what means it is possible to determine the geographical point of origin of any particular plant group. This information may clearly be of great importance to the plant geographer,

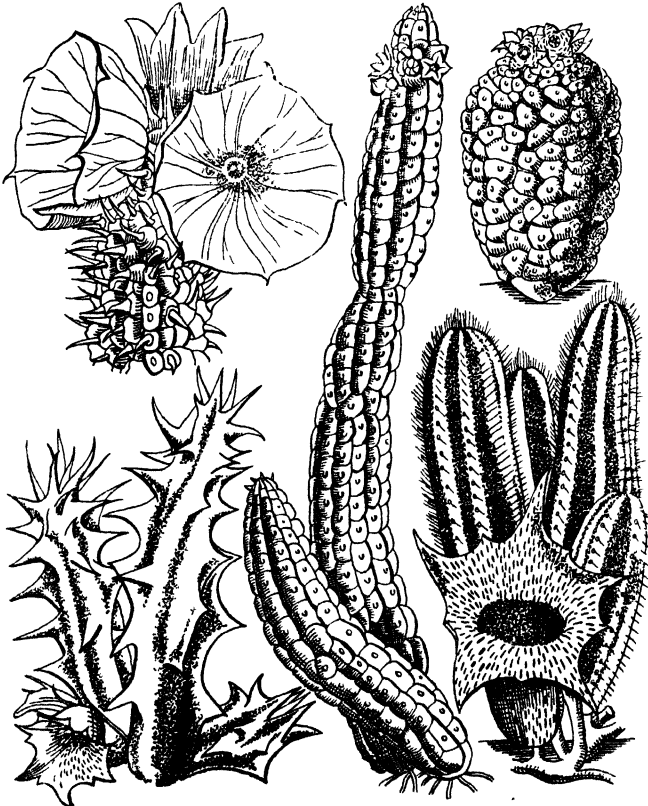


FIG. 46.—Some characteristic members of the tribe Stapelieae, after Wettstein.

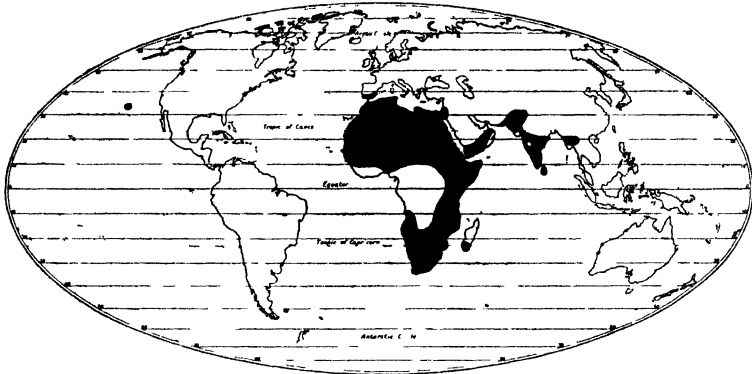


FIG. 47.—Map showing (black) the distribution of the tribe Stapelieae. The small white spot in the Indian Peninsula marks the distribution of the genus *Frerea*

and much attention has therefore been given to the consideration of the possible criteria and evidences by which it may be indicated. It is beyond the scope of this chapter to discuss these suggestions in detail and for such a treatment reference should be made to the very full account given by Cain (276), but the application of some of these additional criteria may be illustrated by a short account of the Stapelieae, a tribe of the family Asclepiadaceae. This group of twenty genera has been monographed on an elaborate scale (258) and its geography can therefore be described with some confidence.

The Asclepiadaceae are, as a family, characterised by marked specialisation of flower structure, but the Stapelieae add to this an equally specialised vegetative form, being one of the three main groups of flowering plants (the others being the Cactaceae and certain Euphorbias) which, in association with desert habitats, have developed a Cactoid habit, that is to say, which have lost their leaves and developed stems which are green, succulent and commonly more or less angularly cylindrical.

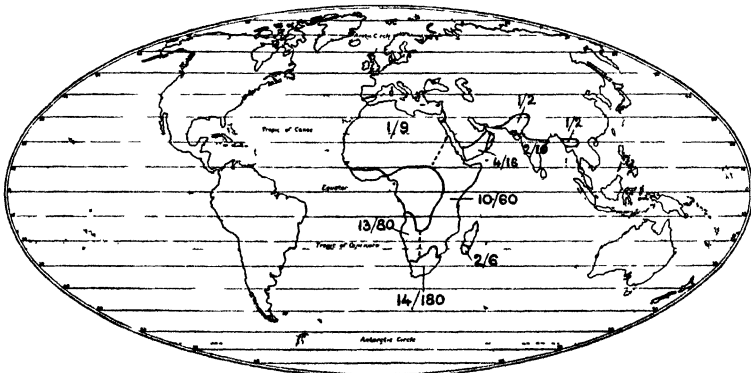


FIG. 48.—Map showing the numbers of genera/species in different parts of the range of the tribe Stapelieae.

The geography of the Stapelieae is shown vividly in figs. 47, 48, and it is only necessary here to summarise the chief points of importance. These are:

1. The group as a whole ranges from Burma to Senegal and down the east side of Africa to the Cape.
2. Of its 370 species more than 280 are found only in South Africa.
3. No fewer than twelve out of twenty genera are found only in southern Africa and Madagascar.
4. One genus, *Caralluma*, has the range of the whole group.
5. This genus has half its 110 species in South Africa; four in East Africa; about thirty round the mouth of the Red Sea; and nearly all the rest scattered along its main west-east axis.
6. Eighteen out of the remaining nineteen genera are restricted to south Arabia, East Africa, South Africa, and very slightly to Madagascar.
7. The only other genus, *Frerea*, is a monotype of very restricted range in the vicinity of Poona in India.

Here, then, is a large group of plants numerically centred in South Africa but ranging widely therefrom both north and east. At first sight it might therefore be supposed that the group originated in South Africa and spread thence, but, as will be seen, there is strong evidence that the contrary is true.

The evidence for this view resides chiefly in the relationship between the different genera of the group. For reasons which need not be considered in detail here it is generally and quite justifiably believed that extremely specialised structural modifications towards life under markedly xerophytic conditions, as in deserts, have been comparatively recently derived from more mesophytic types with more ordinary form and possessing leaves. For these reasons, for instance, *Pereskia*, which is the only genus of Cactaceae with leaves, is generally held to be the most primitive type of the family. It is therefore interesting to find that there is one genus of Stapelieae which has leaves and which is far less xeromorphic than the others, and which therefore may be regarded as the most ancient and primitive of the group, and still more interesting to find that this is the genus *Frerea*, the Indian monotype. Again, *Caralluma* is certainly the most generalised of the xeromorphic genera, and this is the only other genus found east of Arabia. Still again, the general relationship of its species is along the line from Burma to Senegal, and the South African branch of its range is occupied by its most specialised species. Finally, the South African genera are all to be regarded as among the most specialised of the whole group.

In short, all the evidence seems to show that the Stapelieae are of Asiatic origin and that their extension down the east side of Africa is a branch of their main geographical axis. If this is so, then the group illustrates, not a maximum species concentration at its point of origin, but one at the point furthest from it, and, however much the general distribution of the species may, at first sight, suggest a South African origin for the group, the other lines of evidence are all in favour of the contrary view.

It seems clear then, at least from this example, that, unless it is supported by other evidence, a great local concentration of species cannot necessarily be held to indicate the original home of a plant group, but that every group showing such a concentration must be considered on its merits.

CHAPTER 9

THE DISTRIBUTION OF SPECIES—II

It has already been pointed out that there is no fundamental distinction between the ranges of genera and the ranges of species, and, this being so, it is practicable and convenient to use, in this and the next two chapters, the same general classification of distributional types as was employed in the case of genera, beginning with the most widespread forms and working down to the most restricted endemics. To the former class this chapter is devoted.

Cosmopolitan and Very Wide Species

It can be said with certainty that no species is cosmopolitan in the sense that it occurs naturally wherever flowering plants will grow, but a good many are so widely distributed that they do not fall into any more restricted category.

Such species tend to fall into three classes: they are fresh-water aquatics, or temperate species now widely adventive in the tropics, or they are tropical species to some extent adventive in more temperate regions.

Apart from these sorts there are few really widely spread species, and indeed *Prunella vulgaris* and *Luzula campestris* are perhaps the only ones which merit particular mention. These seem to be natives over exceptionally wide areas.

Actually *Phragmites communis*, the common reed, is generally quoted as the most widely distributed of all Angiosperms. It occurs, often in great quantity, in nearly all parts of the world, but is said by Ridley (202) to be absent from the region of the Amazon. It is, however, an aquatic plant and may well serve as an introduction to the other species comprising the first of the three types mentioned above.

Darwin (52) was one of the first to call attention to the exceptional range of many fresh-water aquatic species (especially those that live floating or submerged) and paid considerable attention to them.

Among them the members of the genus *Lemna* are nearly all very widespread, but their peculiar growth-form tends to favour casual transport of whole plants such as is scarcely known elsewhere, and their geography certainly owes something to this.

This is certainly not true, however, of *Potamogeton pectinatus*, which shows an equally wide range. *Typha latifolia* and *T. angustifolia* are similarly widespread, the former being absent only from central and southern Africa and the latter from North America and Madagascar.

Among other wide aquatics are *Ceratophyllum demersum*, *Cladium Mariscus*, *Cyperus flavescent*, *Glyceria fluitans*, *Hippuris vulgaris*, *Lythrum Salicaria*, *Myriophyllum spicatum*, *Najas marina*, *Nasturtium officinale*, *Phalaris arundinacea*, *Scirpus* spp. and *Zannichellia palustris*.

Others almost equal in range, but which are less widespread in the temperate regions, include *Rotala mexicana*, *Ammannia auriculata* and *Ludwigia parviflora*.

It must be remembered that aquatic plants have generally, although they may be well scattered, a comparatively limited area of actual occurrence, so that while the total area may be wide the number of individuals may be much less than in the case of more restricted species. This kind of limitation of habitat, as opposed to total range, is also seen in the case of other plants of various special kinds, prominent among them being the halophytes, of which *Suaeda maritima*, *Salicornia europaea* and *Salsola Kali*, are generally credited with an almost world-wide distribution. They do indeed occur in all latitudes, but their edaphic requirements (see Chapter 17) limit them either entirely or largely to coastal areas or to where inland there are salt deposits, so that the actual size of the area they cover is relatively small. The same thing is true of many temperate species in the tropics. Their occurrences may be widely scattered, but at least if they inhabit very high altitudes the total area they cover may be very small.

The next two types both involve the problem of status (see Chapter 12), and this in particular prevents more than a rather indefinite account of these very widespread species because they may often be no more than transitory casuals.

As regards these partially adventive weeds it is instructive to notice that those introduced from temperate to tropical regions have for the most part wider ranges than those in which the movement has been the reverse, which seems to indicate that while many species can live, under somewhat artificial conditions, in surroundings considerably warmer than those to which they are normally accustomed, few can maintain themselves in conditions much colder than the normal. Here two factors are certainly concerned deeply: in colder regions the growing season is shorter and there is less chance of ripening seed, but more important is the fact that the temperate zones nearly everywhere have frost at one time or another, a condition to which tropical plants are not exposed.

It is probably true to say that all temperate weeds find niches somewhere in the tropics as a result of carriage by man, but the following appear to be particularly ubiquitous:

Capsella Bursa-pastoris, *Chenopodium album*, *Erigeron canadensis*, *Euphorbia Helioscopia*, *Plantago major*, *Poa annua*, *Polygonum aviculare*, *Solanum nigrum*, *Sonchus oleraceus*, *Stellaria media*, *Taraxacum officinale* and *Urtica dioica*.

The opposite condition of tropical species extending into more temperate zones as weeds is shown well by the following, of which some actually occur rarely in the British Isles:

Amaranthus Blitum, *Asclepias curassavica*, *Cynodon Dactylon*, *Echinochloa crus-galli*, *Gnaphalium luteo-album*, *Paspalum distichum*, *Portulaca oleracea* and *Setaria verticillata*.

Pan-tropical Species

The number of species which to-day are found practically throughout the tropics is large, but here again it is very difficult to determine their status in different parts of the world. A few perhaps have, as will be seen, a natural range over the tropics, but the vast majority of them have been introduced widely and especially between the western and eastern hemispheres. Some have been actually planted all over the tropics, like the coconut, whose place of origin is still a matter of argument; some have run wild from cultivation; while still others, and these seem most numerous, are weeds of tropical lands occurring like those of the temperate zones wherever there is disturbed ground, though each is native to some part of its range.

The relative absence of natural pan-tropical species has often been commented

on, and Ridley (202) calls attention to the fact that the nearest approach to them appears to be such members of the Cyperaceae as *Cyperus Haspan*, *Fuirena umbellata*, *Eleocharis geniculata*, *E. Chaetaria*, *Rhynchospora corymbosa* and *Scleria lithosperma*. It is fairly certain that these plants at least are not adventives, but with almost all other pan-tropical species there is generally some reason for suspicion.

Among the widely found escapes from cultivation in the tropics are *Acacia Farnesiana*, *Amaranthus caudatus*, *Anacardium occidentale*, *Cajanus Cajan*, *Canavalia ensiformis*, *C. maritima*, *Gossypium arboreum*, *G. peruvianum*, *Physalis peruviana* and *Tamarindus indica*.

The widely distributed tropical weeds are of general interest from many points of view, and for this reason the following list of some of the most important is not too long :

<i>Abrus precatorius</i>	<i>Evolvulus alsinoides</i>
<i>Abutilon asiaticum</i>	<i>Gomphrena globosa</i>
<i>A. crispum</i>	<i>Gynandropsis gynandra</i>
<i>A. hirtum</i>	<i>Gyrocarpus Jacquinii</i>
<i>A. indicum</i>	<i>Heteropogon contortus</i>
<i>Achyranthes aspera</i>	<i>Hibiscus cannabinus</i>
<i>A. indica</i>	<i>H. Sabdariffa</i>
<i>Ageratum conyzoides</i>	<i>Hyptis pectinata</i>
<i>Amaranthus spinosus</i>	<i>Jussiaea repens</i>
<i>A. tristis</i>	<i>J. suffruticosa</i>
<i>Bidens leucantha</i>	<i>Lantana mixta</i>
<i>Bryophyllum pinnatum</i>	<i>Leonotis nepetifolia</i>
<i>Caesalpinia Bonduc</i>	<i>Leucas martinicensis</i>
<i>C. pulcherrima</i>	<i>Limnocharis flava</i>
<i>Capsicum frutescens</i>	<i>Microglossa pyrifolia</i>
<i>Cassia Absus</i>	<i>Mikania scandens</i>
<i>C. Tora</i>	<i>Mimosa pudica</i>
<i>Cassytha filiformis</i>	<i>Mucuna pruriens</i>
<i>Catharanthus (Lochnera) roseus</i>	<i>Oxalis rosea</i>
<i>Celosia argentea</i>	<i>Peperomia reflexa</i>
<i>Cenchrus echinatus</i>	<i>Phyllanthus distichus</i>
<i>Coix Lacryma-Jobi</i>	<i>Pisonia aculeata</i>
<i>Commelina diffusa</i>	<i>Sesuvium portulacastrum</i>
<i>Cressa cretica</i>	<i>Sida cordifolia</i>
<i>Crotalaria incana</i>	<i>S. rhombifolia</i>
<i>C. retusa</i>	<i>S. spinosa</i>
<i>Cyathula prostrata</i>	<i>S. urens</i>
<i>Desmodium triflorum</i>	<i>S. veronicifolia</i>
<i>D. umbellatum</i>	<i>Sigesbeckia orientalis</i>
<i>Digitaria sanguinalis</i>	<i>Solanum aculeatissimum</i>
<i>Dodonaea viscosa</i>	<i>Spilanthes Acmella</i>
<i>Eclipta prostrata</i>	<i>Tragus racemosus</i>
<i>Eichhornia crassipes</i>	<i>Urena lobata</i>
<i>Elephantopus scaber</i>	<i>Vigna marina</i>
<i>Eriodendron anfractuosum</i>	

It may be noted that in this list the families Malvaceae, Amaranthaceae, Leguminosae, Compositae and Gramineae are particularly well represented, and that some of the species are strand-plants (see Chapter 11).

Other Wide Species

Northern temperate species

Here, again, the complication of intentional or accidental introduction is prominent because so many plants have been introduced from Eurasia into North America that it is not always easy to tell which species have naturally a completely circumboreal distribution. It must also be remembered that arctic plants are also, if they are widespread, circumpolar, and it is difficult to draw any hard and fast line which can exclude them.

Naturally many completely northern temperate plants will occur in the British Isles and will be therefore more or less familiar, and from these the following, which illustrate the category fairly well, may be cited :

Achillea Millefolium, *Anemone nemorosa*, *Caltha palustris*, *Campanula rotundifolia*, *Gentiana Pneumonanthe*, *Myrica Gale*, *Nuphar lutea*, *Oxalis Acetosella*, *Parnassia palustris*, *Pinguicula vulgaris*, *Ribes rubrum*, *Rumex Acetosa*, *Vaccinium Myrtillus* and *Vicia Cracca*.

The fact that northern temperate species extend often into the tropics at one point or another is illustrated by *Solidago Virgaurea*, which is found in Formosa and the Philippines.

Mertensia maritima is a particularly interesting case of a plant linking this category with the arctic. It occurs from Japan, across the northern and arctic part of North America to north-western Europe. This plant also serves to link up with another type of distribution which must be dealt with here, namely the North Pacific or Bering type.

Typically, what are here called North Pacific species (see fig. 49) range only over north-eastern Asia and north-western North America, and such are *Harrimanella Stelleriana*, *Echinopanax horridum*, *Phyllodoce aleutica*, *Cassiope lycopodioides* and one or two violets. There are, however, in addition a number of species which, while widely distributed in North America, actually extend for varying distances across the Bering Straits into Asia. *Mitella nuda*, for instance, is found all over North America as well as in north-east Asia. These plants are an important part of what Hulten (132) has called "the American component in the flora of Eastern Siberia," and he has given an interesting account of them from which further details may be obtained.

There are also examples of the opposite state of affairs, where the bulk of the distribution is Asiatic, but on the whole there seems little doubt that the first type predominates, suggesting that migration across the Straits has been chiefly from the American side.

Eurasian species

As in the case of genera, it is convenient to treat under this heading many species which have ranges actually falling almost or entirely within the exceptionally wide Euro-Siberian region. Not only would it be misleading to separate them, but it is often difficult to say exactly how far south in eastern Asia a species reaches. For instance, some extend eastward only through Siberia, while many others occur in Japan.

There are a number of fairly familiar plants of cultivation with (though it is not always complete) this type of range, and among them are *Asparagus officinalis*,



FIG. 49.—Map showing the distribution of the genera *A. Bryanthus*, *B. Harrimanella*, *C. Cassiope* and *D. Phyllodoce*.

Campanula Trachelium and *Syringa vulgaris*. *Narcissus Tazzetta* is said to occur from the Canaries to Japan.

Many British plants also may be cited as examples, and among them the following range more or less completely through the Eurasian temperate zone, some, at least, to Japan :

Angelica sylvestris, *Cirsium arvense*, *Conium maculatum*, *Convolvulus arvensis*, *Geranium pratense*, *Heracleum Sphondylium*, *Holcus lanatus*, *Lamium album*, *Listera ovata*, *Ranunculus acris* and *Rubus idaeus*.

Sanicula europaea extends south into the African mountains and into Malaya, and *Brachypodium sylvaticum* also reaches the latter.

There are also, of course, many species ranging from Europe eastwards which do not happen to occur in Britain.

Old World tropical species

Reference is often made in the literature to species which are described as having a distribution throughout the Old World Tropics, with the inference that they are more or less continuous from southern Africa to the Pacific Islands. Probably there are very few if any species which naturally have this range rather than one which falls more appropriately into one or other of the next two categories, but there is certainly a group of species which generally, owing to introduction here or there, or to escape from cultivation, have this range in a more or less complete form. They are therefore to be regarded as the counterpart on a smaller scale of the pan-tropical weeds already discussed, and a short list of some of the more important is of interest. It contains:

Bryonopsis laciniosa, *Canscora diffusa*, *Carapa moluccensis*, *Conyza aegyptiaca*, *Cymbopogon citratus*, *Dichanthium annulatum*, *Diplachne fusca*, *Drosera indica*, *Elytrophorus spicatus*, *Gymnema sylvestre*, *Hibiscus aristivalvis*, *H. caesius*, *H. panduriformis*, *H. surattensis*, *H. Trionum*, *Imperata cylindrica*, *Musa Cavendishii*, *M. paradisiaca*, *Ocimum Basilicum*, *Parochetus communis*, *Polygonum plebeium*, *Portulaca quadrifida*, *Rottboellia exaltata*, *Solanum Melongena*, *S. Pseudocapsicum*, *Sphaeranthus africanus*, *S. indicus*, *Tacca Leontopetaloides*, *Trichodesma zeylanicum*, *Xyris indica*.

African-Asiatic species

As has just been indicated, the wider naturally ranging species of the Old World tropics are either found from Africa to Asia or from Asia to Australasia and the Pacific Islands, and the present category contains the former.

For the most part they are rather xerophilous species, because otherwise they tend to be absent from northern Africa and western Asia and therefore to be discontinuous, but they include quite a number of others as well. Again, most of them range from Africa only as far as India or southern China, but others extend far into Malaya. Some, too, occur in Madagascar or the Mascarenes as well as in continental Africa.

It will thus be seen that the category is not well defined, but a range of this kind has been attributed to *Aerva javanica*, *Arthraxon lancifolius*, *Cleome monophylla*, *Desmostachya bipinnata*, *Hypericum Lalandii*, *Latipes senegalensis*, *Pavonia Schimperiana*, *Polygala erioptera*, *Rumex nepalensis*, *Schismus barbatus*, *Sorghum subglabrescens*, *Urochloa panicoides*.

Asiatic-Australasian species

This category is to be regarded as the counterpart of the last and as containing, in particular, those species which range all the way from continental Asia to Australasia or the Pacific Islands, though there are some that do not appear further west and north than the Malayan Archipelago.

The commonest distribution is from India to northern Australia, thus covering one of the main climatic, and especially rainfall, areas of the world, and examples of this range are afforded by *Deeringia amaranthoides*, *Epipogium roseum*, *Hoya carnosae*, *Mimusops Balata*, *Pholidota imbricata*, *Pluchea indica* and one or two *Droseras*, but there are many other types also which may be illustrated by the following random instances:

<i>Lagenophora Billardieri</i> , <i>Zoisia Matrella</i>	. Asia to New Zealand.
<i>Malaisia tortuosa</i>	. Asia to Polynesia.
<i>Morinda citrifolia</i>	. Asia to Australia and Polynesia.
<i>Danthonia pilosa</i>	. Java to Australia.
<i>Haloragis micrantha</i>	. Asia to Australia and New Zealand.
<i>Microtis unifolia</i>	. Liu Kiu Islands to Australia.
<i>Caladenia carnea</i>	. Malaya to Australia and New Caledonia.

Indo-Malayan species

It is no exaggeration to say that the Indo-Malayan flora is, in many respects, one of the most interesting of the whole world, as well as being one of the richest (frontispiece), but space will not allow of more than a passing reference to some of its outstanding features.

Not only is it a very well-marked unit but it has provided many plants of considerable importance to the human inhabitants of the region, and many familiar species are either characteristic of it or are thought to have had their original home somewhere within it. Among them may be mentioned *Adenanthera pavonina*, *Areca Catechu*, *Artocarpus integer*, *Boehmeria nivea*, *Durio zibethinus*, *Mangifera indica*, *Nephelium lappaceum*, *Palaquium Gutta*, *Piper Betle*, *Piper Cubeba*, *Pogostemon Patchouly*, *Tectona grandis* and *Uncaria Gambier*.

The botanical history of the region also is a subject of great interest, especially with regard to the inter-relationships of the different parts, and this has been discussed very fully by Van Steenis (249) in connection with the montane floras of the Malayan Archipelago. This work will be mentioned again later, but it may be noted here that the distribution of species shows two very distinct lines of relationship between the Archipelago and the Asiatic continent, one by way of India, Indo-China, Java and Sumatra, and another by way of China, Japan, Formosa and the Philippines.

The former line is illustrated by the distributions of *Anemone sumatrana*, *Bucklandia populnea* and *Thalictrum javanicum*, and the latter line by *Androsace umbellata*, *Asparagus cochinchinensis* and *Skimmia japonica*.

Apart from these, however, there is almost every other kind of distribution over the region as a whole, as the following examples (which are taken from Van Steenis) show :

<i>Pratia montana</i>	. India and China to Java.
<i>Aster trinervis</i>	. India and Japan to the Philippines.
<i>Senecio Wallichii</i>	. India to Celebes.
<i>Senecio scandens</i>	. India, Formosa, Philippines, Celebes.
<i>Gaultheria fragrantissima</i>	. Asia to New Guinea.
<i>Swertia bimaculata</i>	. India, Japan and Sumatra.
<i>Euchoesta Horsfieldii</i>	. India, Philippines, Java.
<i>Anemone vitifolia</i>	. Himalayas to Philippines and Formosa.
<i>Fragaria indica</i>	. Asia to Philippines and Java.
<i>Ellisiophyllum pinnatum</i>	. India to Japan, Formosa, Philippines.
<i>Hemiphragma heterophyllum</i>	. India, China, Formosa, Philippines, Celebes.

There is also a marked linkage between the Archipelago and north-eastern Asia, exemplified by:

<i>Actinidia callosa</i>	.	.	.	north-east Asia to Java.
<i>Artemisia capillare</i>	.	.	.	Manchuria to Philippines.
<i>Liriope graminifolium</i>	.	.	.	Manchuria, Annam, Formosa, Philippines.

Wide African species

Under this heading must be included the various types of distribution too wide to be included under any one of the African regions, and here again, as so often before, almost any particular range can be exemplified, but there are certain predominant types.

One comprises species found widely in Africa, or at least the tropics, and also on the islands. Examples of this are furnished by *Celosia trigyna*, *Harungana madagascariensis* and *Sorghum verticilliflorum*.

Much more familiar and numerous are some of the plants which range widely over the continent itself. An extreme condition is seen in such plants as *Clematis simensis* or *Oncoba spinosa*, which actually reach Arabia, but the great majority are found only south of the Sahara, although *Priva cordifolia* and doubtless some others extend from Socotra to the Cape.

A few wide African species like *Coleus thyrsoides*, *Kalanchoe coccinea* and *Zantedeschia aethiopica* (the arum lily) are grown in greenhouses, and the last is perhaps the best-known of all African plants. There are also a few economic plants of at least local importance which now have a wide range. Among them may be mentioned *Butyrospermum Parkii*, *Cola nitida*, *Pentadesma butyraceum*, *Ricinus communis*, *Sorghum caffrorum*, *S. guineense* and *Voandzeia subterranea*.

For the rest the following is a selection of the species to which a wide distribution in tropical or warm Africa has been attributed:

Adansonia digitata, *Baphia nitida*, *Clematopsis scabiosifolia*, *Cleome hirta*, *Clerodendrum Thompsonae*, *Cymbopogon giganteus*, *Hypericum Roeperianum*, *Leonotis Leonurus*, *Nymphaea caerulea*, *Pennisetum purpureum*, *Pluchea Dioscoridis*, *Sorghum arundinaceum*, *Sparrmannia africana*, *Stephania abyssinica* and *Telfairia pedata*.

Australian and New Zealand wide species

Here two rather distinct types of distribution find a place, namely the wide Australian, which covers more than one of the regions into which the continent is divided, and the Australian-New Zealand type, which is discontinuous but which it is convenient to consider here. In addition there may be included the species which are almost exclusively in Australia or New Zealand but which have in fact some representation in the eastern parts of the Malayan Archipelago. These latter may be dismissed at once with the remark that they are exemplified by:

<i>Erechtites arguta</i>	.	.	.	Australia, New Zealand, New Guinea, and the Lesser Sundas.
<i>Uncinia riparia</i>	.	.	.	Australia, New Zealand, New Guinea and Borneo.
<i>Carpha alpina</i>	.	.	.	Australia, New Zealand and New Guinea.
<i>Geranium pilosum</i>	.	.	.	Australia, New Zealand and New Guinea.
<i>Eulophia nervosa</i>	.	.	.	Australia and New Guinea.



Plate 12. *Protea cynaroides* at the Cape

As regards the species widely distributed within the continent their range usually takes one of two forms ; they are either plants of the drier interior which actually extend into one or other of the peripheral regions or they are plants which extend more or less completely across the south of the continent from east to west. The former includes a number of grasses, among them *Panicum decompositum*, *Pappophorum nigricans* and *Triodia irritans*.

The latter are certainly much more numerous, and almost every large and characteristic Australian genus contains one or more of them, though the proportion is always small. *Casuarina distyla*, *Goodenia pinnatifida*, and a number of species of *Eucalyptus* and *Grevillea* are examples.

There is a strong element of relationship between the floras of Australia and New Zealand and the two regions appear to have at least 220 species in common. Among those which are found only in these two countries may be mentioned *Mazus pumilio*, *Scleranthus biflorus*, *Spinifex hirsutus* and *Stipa teretiflora*.

American wide species

It would take far more than the space available here to give even a brief complete survey of the innumerable types of wide distribution exhibited in the huge area of the New World. The task is, moreover, made particularly difficult because of the absence of barriers between the north and south and the facilities for plant movement in this direction afforded by the long chain of the western mountains, and, as a result of these conditions, there is every variation in latitudinal plant distribution. All that can be done is to supplement what will be said later under the various regions. With this purpose in view we may pass somewhat rapidly over certain aspects by saying that there are species like *Erechtites hieracifolia* which are said to occur practically all over America, *Madia sativa* which occurs all down the west side, and others such as *Apocynum androsaemifolium*, *Dodecatheon Meadia*, *Symphoricarpos albus*, and various species of *Penstemon*, *Solidago*, *Trillium* and *Carya* which range widely through North America, and pass on to the more detailed and necessary consideration of the widely spread tropical species.

In one sense the tropical portion of America corresponds to the whole of the Old World tropics and may be expected to have in the same way its own widely distributed weeds and denizens. This is so, and in order to make a comparison between the two hemispheres possible it is worth while to give a fairly extended list of the species which are more or less completely distributed now through the New World tropics. The list includes also some of the species whose natural ranges are especially wide, as well as a few species now so widely cultivated that their place of origin can hardly be decided.

Bocconia frutescens
Bursera gummiifera
Capsicum annuum
Carica Papaya
Cedrela odorata
Chlorophora tinctoria
Chondodendron tomentosum
Clidemia hirta
Cordia Sebestena
Crataeva Tapia

Cyathula achyranthoides
Desmodium adscendens
Epidendrum fragrans
Epidendrum nocturnum
Epidendrum rigidum
Erythrina Corallodendrum
Flaveria Contrayerba
Gossypium barbadense
Hura crepitans
Inga vera

Jatropha Curcas
Jatropha pungens
Jussiaea peruviana
Maranta arundinacea
Mirabilis Jalapa
Mollugo verticillata
Ochroma Lagopus
Oncidium luridum
Peperomia hispidula
Peperomia rotundifolia
Phaseolus multiflorus
Piper aduncum

Piptadenia peregrina
Psidium Guajava
Pterocarpus officinalis
Rivina humilis
Seraphyta diffusa
Simarouba amara
Spigelia anthelmia
Spondias purpurea
Tecoma stans
Trema micranthum
Tribulus cistoides

Among species less widely distributed in the American tropics nearly every possible range can be exemplified. A very common one is that of plants common to the West Indies and to the northern part of the South American mainland, often to Venezuela or Guiana only, and among these are *Cecropia peltata*, *Guajacum officinale*, *Mammea americana*, *Oncidium pulchellum* and *Pleurothallis pruinosa*.

Another group has a similar range but extends farther into South America, as, for instance, to Brazil, and here belong *Erythrina velutina*, *Galeandra Beyrichii* and *Hedyosmum arborescens*.

Another rather frequent type includes the species which, found in both Central America and the West Indies, also occur in the northern part of South America. Examples of these are *Hippomane Mancinella*, *Lonchocarpus latifolius* and *Rubus alpinus*.

Many plants are widely distributed in South America proper but do not reach either Central America or the West Indies, and these include *Bixa Orellana*, *Hymenaea Courbaril* and *Lucuma mammosa*.

Brassavola nodosa and *Phyllanthus caroliniensis* are instances of species which are found in Central America and the West Indies and also on the western (Andine) side of South America.

As might be expected from the absence of any marked physical barriers, many plants are in South America found partly in the tropics and partly in the temperate regions. As the following list shows, they include several well-known plants, namely, *Bertholletia excelsa*, *Fuchsia magellanica*, *Ilex paraguayensis*, *Lippia citriodora*, *Nicotiana noctiflora*, *Nicotiana Tabacum*, *Strychnos toxifera*, *Theobroma Cacao* and *Tropaeolum majus*.

The floral relationship between the north temperate regions and the north tropics is best left for discussion in the next chapter, but this one may be closed by a mention of *Geranium carolinense*, which is said to occur in both Central America and the West Indies, and northward as far as Canada.

CHAPTER 10

THE DISTRIBUTION OF SPECIES--III

Endemic Species

STRICTLY speaking, a narrower conception of endemism should be employed for species than for genera, but to do this here would mean recasting the geographical background in a way which would certainly make for confusion, and for this reason it is better to give the term endemic the same value in both and to treat the endemic species on the same regional basis as was used for the genera. As before, species falling partly into two or more regions are included under the region of which they are most characteristic.

It will be remembered that the proportion of endemic genera among all genera proved to be about 80 per cent. Species have, on the average, much smaller areas than genera, and hence it may be assumed that, on the present conception of endemism, the proportion of endemic species is considerably greater and may well exceed 90 per cent. At all events there have now to be dealt with the vast majority of the species of flowering plants.

Arctic and Sub-arctic Region

In Chapter 7 it was convenient to regard the flora of this region, that is to say the arctic flora proper, as a separate unit, but this is a simplification of the facts which can scarcely be maintained when species are considered.

Actually the alpine flora of the mountains south of the arctic zone is, at various altitudes according to latitude, so similar to that of the arctic region at sea level as really to form with it one whole, namely what is generally called the arctic-alpine flora, and it is this rather than one or other constituent that is the real entity.

Geographically the arctic-alpine flora falls, as is indicated by its name, into two parts, one inhabiting the arctic and the other the mountains outside it, but many species occur in both. There is, moreover, no real spatial segregation, but the verbal differentiation is a useful practical one.

As regards the former component there is unfortunately no complete modern revision of the arctic flora. An early general account of it was given by Hooker (128), but his definition of the arctic flora was not altogether satisfactory and made his statistics less useful than they would otherwise have been, while more modern studies have mostly been confined to one or other of its three geographical divisions, namely the palaearctic (Eurasia), the nearctic (North America), and Greenland.

Some impression can, however, be gained from the fact that the richest constituent flora appears to be that of the last named, which has about 400 species, 13 per cent. of which are said to have been introduced by the early Norse settlers. Of the remainder about four-fifths are of American affinity, and the others of European affinity. It may also be noted that many species are found on both the west and east coasts, and that of the others those found only on the west greatly outnumber those found only on the east.

The question of endemism in the arctic flora proper is a difficult one. Many species are specially characteristic of this region but very few of them are absolutely confined to it, the great majority being also to some extent alpine. Perhaps the most conspicuous endemics are a few grasses, including *Phippsia algida*, *Colpodium fulvum*, *Dupontia Fischeri* and *Pleuropogon Sabinii*. The genus *Braya* includes two or three endemics, as also does *Pedicularis*; while several species of *Salix*, among them *S. arctica*, *S. nummularia* and *S. polaris*, are so described. Other actual or virtual endemics are *Chrysanthemum arcticum*, *Nardosmia glacialis* and *Ranunculus Pallasii*.

Artemisia senjavinensis and *Merckia physodes* occur both in north-east Asia and north-west America and hence, although arctic, form a link with a type of distribution described in the last chapter as North Pacific.

Besides all these, various endemic microspecies have been described, mostly within recent years.

The remaining species of the arctic flora are found also in one or more mountain systems of the northern hemisphere or even occasionally further afield, and constitute the *arctic-alpine* flora proper. Although the distribution in detail of these species is extraordinarily varied, its main outlines can be appreciated fairly easily because of its correlation with the major topography of the northern latitudes.

With some exceptions the elevated regions of the northern temperate zone are aggregated into three great but distinct systems. These are the Rockies in America; the various isolated *massifs* which constitute the mountains of central and southern Europe and which may here be called comprehensively the Alps; and the enormous system of the Himalayas in Asia.

The interesting immediate point about these three systems is that they vary considerably in their distance from the arctic proper. The Rocky Mountains actually fuse with it in the north; the Alps are roughly along the latitude 45° N.; and the Himalayas are roughly between 30° and 35° N. The floristic relationship is closely correlated with this spatial one. Arctic alpine species are most numerous in the Rocky Mountains, fairly numerous in the Alps, but very few in the Himalayas. The significance of these relationships will be considered later, but it is relevant to point out here that the Himalayan region is not only the most isolated from the arctic to-day but was even more markedly so during the Pleistocene ice ages.

As between these four constituent areas, the arctic, the Rockies, the Alps, and the Himalayas, there is almost every kind of specific distribution. It would take too long to describe these in detail, but a good impression of them can be given by quoting the distribution recorded by Hegi (116) for a few of the most familiar plants of the European mountains, as follows:

<i>Androsace Chamaejasme</i>	.	.	.	Alps, Urals, Altai, Himalayas, Arctic.
<i>Anemone alpina</i>	.	.	.	Alps and Arctic.
<i>Atragene alpina</i>	.	.	.	" " "
<i>Bartsia alpina</i>	.	.	.	" " "
<i>Campanula Scheuchzeri</i>	.	.	.	Alps, Altai, Arctic.
<i>Dryas octopetala</i>	.	.	.	Alps and Arctic.
<i>Gentiana nivalis</i>	.	.	.	Alps, Asia Minor, Arctic.
<i>Hedysarum obscurum</i>	.	.	.	Alps and Arctic.
<i>Myosotis alpestris</i>	.	.	.	Alps, Corsica, Arctic.
<i>Polygonum viviparum</i>	.	.	.	Alps, Altai, Himalayas, Arctic.

<i>Ranunculus glacialis</i>	.	.	.	Alps and Arctic.
<i>Ranunculus pygmaeus</i>	.	.	.	Alps, Rockies, Arctic.
<i>Salix herbacea</i>	.	.	.	Alps, Scotland, Urals, Rockies, Arctic.
<i>Saxifraga aizoides</i>	.	.	.	Alps and Arctic.
<i>Saxifraga oppositifolia</i>	.	.	.	" "
<i>Veratrum album</i>	.	.	.	" "
<i>Viola biflora</i>	.	.	.	" "

Certain other familiar plants of the European mountains form as it were a link with the next region to be discussed in being distributed far to the north though scarcely into the arctic proper. Such are :

<i>Arnica montana</i>	.	.	.	widely distributed in Europe and north Asia.
<i>Campanula barbata</i>	.	.	.	in the Alps, Carpathians and Norway.
<i>Gentiana purpurea</i>	.	.	.	" " Norway and Kamchatka.
<i>Lactuca (Mulgedium) alpina</i>	.	.	.	" " and also in north Europe.
<i>Nigritella nigra</i>	.	.	.	" " " "

The species of the genus *Diapensia* also illustrate an interesting state of affairs. According to Evans (74), *Diapensia lapponica* is circumpolar and also found in the White Mountains of eastern North America and in Japan ; while the other three species, *D. himalaica*, *D. purpurea* and *D. Wardii*, are all confined to the eastern parts of the Himalayan system.

The *alpine* flora proper, namely those plants which, while part of the arctic-alpine flora as a whole, are only found in the mountain systems mentioned, is best considered under the regions of which these mountains form part.

Euro-Siberian Region

The more widely spread endemic species of this region have already been dealt with in the preceding chapter, and we have therefore to consider here only those which are more narrowly restricted. These fall into three particularly well-defined groups : firstly, the species restricted to the western part of the region as a whole, namely those of Europe and the Caucasus ; secondly, the species restricted to the eastern part of the region, namely Siberia ; and lastly, the species of the European mountain systems—the alpine flora in its narrowest sense. Since this last is closely related to the arctic-alpine flora, it may therefore be dealt with first while the foregoing pages are still fresh in the mind of the reader.

It is difficult to compare the European alpine flora with others because the extent of the mountains varies so, but it is safe to say that the alpine flora proper is rich and compares favourably with others proportionately. It tends to differ from them, however, because the European mountains comprise a number of isolated massifs and not one continuous range, and for this reason the comparative ranges of the species are of special interest.

The alpine flora is part of the arctic-alpine flora and therefore has a close affinity with that of the arctic itself, but it has also relation with the European lowland flora and, particularly in the more southern mountains, with the Mediterranean flora.

These points can be best illustrated in general by citing the ranges, as given by Hegi (116), of some more of the familiar plants of the Alps proper :

<i>Androsace helvetica</i>	.	.	.	Alps.
<i>Campanula thyrsoidea</i>	.	.	.	"
<i>Carlina acaulis</i>	.	.	.	wide in south and central Europe.
<i>Crocus albiflorus</i>	.	.	.	Alps, Pyrenees, north Apennines, Carpathians, Balkans.
<i>Dianthus alpinus</i>	.	.	.	Alps.
<i>Erinus alpinus</i>	.	.	.	Alps and Pyrenees.
<i>Gentiana acaulis</i>	.	.	.	Alps, Pyrenees, Carpathians.
<i>Gentiana lutea</i>	.	.	.	Alps, Pyrenees, Apennines, Carpathians, Balkans, Corsica, Sardinia, Asia Minor.
<i>Geum montanum</i>	.	.	.	Alps, Pyrenees, Apennines, Carpathians, Balkans, Corsica.
<i>Globularia cordifolia</i>	.	.	.	Alps, Pyrenees, Apennines, Carpathians, Balkans.
<i>Linaria alpina</i>	.	.	.	Alps, Pyrenees, Balkans.
<i>Narcissus poeticus</i>	.	.	.	Alps.
<i>Paradisea Liliastrum</i>	.	.	.	Alps, Pyrenees, Apennines.
<i>Primula Auricula</i>	.	.	.	Alps, Pyrenees, Apennines, Carpathians, Balkans.
<i>Primula glutinosa</i>	.	.	.	Alps and Balkans.
<i>Saponaria ocymoides</i>	.	.	.	Alps.
<i>Sempervivum arachnoideum</i>	.	.	.	Alps, Pyrenees, Apennines, Carpathians.
<i>Trifolium alpinum</i>	.	.	.	Alps, Pyrenees, north Apennines.

The edelweiss, *Leontopodium alpinum*, is said by Hegi to occur in various mountains from the Alps to Japan, but according to Hance (111) this species is confined to the Alps, Pyrenees and Carpathians.

The differential distribution of the species of a single genus is well shown in *Soldanella*. According to Vierhapper (111), there are seven species with the following ranges :

<i>S. alpina</i>	Alps, Pyrenees, Apennines, Cevennes and Dalmatia ;
<i>S. carpatica</i>	northern Carpathians ;
<i>S. villosa</i>	western Pyrenees ;
<i>S. montana</i>	north-eastern Alps, eastern Carpathians and the Balkans ;
<i>S. hungarica</i>	eastern Alps, Carpathians and Balkans ;
and two species in northern Greece.					

One of the most interesting features of the European mountain flora is the occurrence in it of certain isolated genera affording almost the only known temperate examples of families now confined to the tropical regions of the world. By far the most remarkable instance of this is the occurrence in some of the more southerly mountains of Europe of no fewer than three endemic genera of Gesneriaceae, a family which is otherwise one of the most characteristically tropical. One of these plants, generally called *Ramondia pyrenaica*, is familiar to European gardeners, but there are several others also. Hayek (111) has given a good account of them and shows that there are six species in all belonging to three genera. *Ramonda Myconi* (*Ramondia pyrenaica*) is found only in the Pyrenees ; the remaining five all have varying but very restricted distributions in the mountainous parts of the Balkan Peninsula between the longitudes 20°-26° E. and the latitudes 39°-44° N. These five are *Ramonda Nathaliae*, *R. serbica*, *Haberlea rhodopensis*, *H. Ferdinandii-Coburgii* and *Jankaea Heldrichii*.



Plate 13. A Giant Lobelia (L. Rhynchoptalum) of the African Mountains

(from Karsten & Schenck, Vegetationsbilder)

From the more lowland parts of the western portion of the Euro-Siberian region come many species familiar to us either as British plants or as plants of economic or horticultural value, among them being *Digitalis purpurea*, *Fagus sylvatica*, *Laburnum anagyroides* (*vulgare*), *Malva moschata*, *Narcissus Pseudonarcissus*, *Prunus Cerasus*, *Pyrus communis*, *Malus pumila* (*Pyrus Malus*), *Rosa centifolia* and *Trollius europaeus*. The grape vine, *Vitis vinifera*, may also have had its origin here, perhaps in the Caucasus.

Naturally the plants of the eastern part of the region are less familiar than those just mentioned, but there are a number either grown in gardens or of some other interest which are natives of Siberia or of the immediately adjoining regions. Among these are *Allium sativum*, *Bergenia cordifolia*, *Bergenia crassifolia*, *Delphinium grandiflorum*, *Iris sibirica*, *Lychnis chalconica*, *Pyrus baccata*, *Sium Sisarum* and *Stachys Sieboldii*.

Finally there may be mentioned among other natives of the region, but as having less restricted and well-defined distributions, *Artemisia Abrotanum*, *Echinops sphaerocephalus*, *Gypsophila paniculata* and *Lonicera Xylosteum*.

Sino-Japanese Region

For two reasons in particular this region is one of the most interesting from the point of view of its species. The first is that its flora is extremely rich and almost certainly the richest of the whole northern temperate zone. It is also especially rich in trees and it has, indeed, been said that the number of tree species here outnumbers that of the whole of the rest of the northern temperate zone. Its endemism is also high, but this is only to be expected from the size of the area. It is in relation to what we believe to have been the history of the region that its richness in species and particularly in trees is so significant.

As will be shown in Chapter 14, the great polar ice-cap of the Pleistocene was not, as at first sight might be expected, symmetrical about the present North Pole but had its centre in what is now the southern part of Greenland. As a result the ice reached particularly low latitudes in eastern North America and in Europe, but covered only the northern edges of Asia and, in fact, made itself felt there little more than does the ice-cap of to-day. It will also be seen that there is good reason for believing that prior to the Pleistocene a single great flora, characterised by the prevalence of woody types, was found throughout the northern temperate regions or at least at the lower latitudes. In view of these facts it is therefore justifiable to suggest that the flora of eastern Asia was little affected by the Pleistocene Ice Ages, and hence that the present Sino-Japanese flora is in fact a relatively little-changed descendant of it, giving a picture of the kind of vegetation which, before the glaciation, encircled the whole northern hemisphere.

The second reason for the interest of the flora of this region lies in the fact that of recent years it has contributed an enormous number of plants to European gardens. Indeed, the story of the exploration of the remoter parts of the Himalayas and China by collectors in search of seeds and plants of aesthetic value is one of the romances of twentieth-century botany and geography. It is the story especially of the hitherto little-known mountainous country in the region of the great river gorges near the junction of Burma, China, India and Tibet, and from it the names of Henry, Farrer, Forrest, Kingdon Ward and many others will always be inseparable. The result of their labours and travels has been the discovery not only

of many most valuable garden plants but also of much other botanical and geographical information culminating in the recognition of this part of the world as one of its most remarkable natural features.

The Sino-Japanese region too has contributed greatly to the list of important economic plants, or at least we may say that many such plants had their origin as crops in this region. It is necessary to adopt this somewhat cautious expression, because where a considerable number of cultivated plants are found to have originated there is a rather natural tendency to assume that the local native flora has proved of special value to man as compared with that of other regions. This, it need hardly be said, is an assumption which may not always be justified, and the number of cultivated plants may be a measure of the length of human history rather than any inherent virtue in the flora as a whole.

It is worth discussing this point at some length, because it has often been observed that the important economic plants of the world come especially from certain parts of it and, as often suggested on this basis, especially recently by the Russian school of botanists led by Vavilov (250), that this circumstance has had an important controlling effect on the distribution and growth of human races. Interesting as this view is, it seems to confuse cause and effect. The early civilisations of the world must have originated to a considerable extent independently of one another, if only because of the virtual absence of long-distance communication, and as each passed from a nomadic or pastoral stage to an agricultural level each must have derived its economic plants from local wild plants. In other words, the early peoples must of necessity have made use for the purposes of agriculture of the plants which were immediately available to them. The longer the history of the human population of any region the more complete would be the exploitation of its native plant life in this way, and it is natural to-day, therefore, to find that the areas from which economic plants particularly derive are those with the longest history of human settlement. It is true that certain types of vegetation and therefore certain regions provide a greater selection of potentially valuable plants, but any suggestion that the cultivation of these plants was the cause rather than the effect of human settlement bristles with difficulties.

It is noteworthy too that in different parts of the world there are different but corresponding economic plants. Almost all aspects of economic botany will illustrate this, but it is perhaps outstanding in the case of the three plants, tea, coffee and cocoa, from which important beverages are prepared. Tea is a native of warm Asia, coffee of Africa, and cocoa of South America. Clearly the peoples of each of these continents have, as occasion demanded, developed their own particular beverage from the most suitable available native plant. They have made use of such plants as were available in the circumstances of their situation.

Moreover, once a plant is in cultivation it, so to speak, loses its nationality and can within certain obvious limits be grown as and where required, and there is no necessity for population to remain closely associated with its point of origin. For example, the New World has provided man with several economic plants of first importance, but the fact that these are natives of America has not made it necessary for human population to concentrate there in order to enjoy them.

But to return to the Sino-Japanese flora, there are within the region many types of specific distribution. Some species like *Clematis montana*, *Iris ensata*, *Panax Schinseng*, *Rosa rugosa* and *Diervilla (Weigela) florida* are widespread, or at least their original homes cannot now be more accurately determined.

Many others occur particularly or exclusively in China and Japan, among them being *Anemone japonica*, *Aucuba japonica*, *Callistephus chinensis*, *Camellia japonica*, *Hydrangea macrophylla*, *Lilium tigrinum*, *Parthenocissus tricuspidata* (*Ampelopsis Veitchii*), *Paulownia tomentosa*, *Pyrus pulcherrima*, *Rosa Wichuraiana* and *Saxifraga sarmentosa*. The prototypes, too, of cultivated *Chrysanthemums* are also supposed by most authorities to belong here.

Of plants native to China there may be mentioned *Aspidistra elatior*, *Diospyros Kaki*, *Forsythia suspensa*, *Jasminum nudiflorum*, *Kerria japonica*, *Lonicera nitida*, *Morus alba*, *Primula sinensis*, *Rosa Banksiae*, *Rosa omeiensis* and *Wisteria sinensis*.

Among natives of Japan are *Dicentra spectabilis*, *Fatsia japonica*, *Hamamelis japonica*, *Lilium auratum*, *Lilium longiflorum*, *Magnolia Kobus*, *Primula japonica*, *Rosa multiflora* and *Schizophragma hydrangeoides*.

The debt which the horticulturist owes to the plants of the Himalayas is well shown by *Cotoneaster frigida*, *Erigeron multiradiatus*, *Gentiana Farreri*, *Gentiana sino-ornata*, *Incarvillea Delavayi*, *Magnolia Campbellii*, *Meconopsis betonicifolia* (*Baileyi*) and *Primula Bulleyana*, all of which are native to that zone.

Lastly, *Glycine Max* (*Soya*) and *Caragana arborescens* come from the Manchurian part of the region, and *Fagus Sieboldii* and *Zelkova serrata* from Korea and Japan.

Western and Central Asiatic Region

Botanically the western part of this region, namely north Persia and the interior of Asia Minor, is much the richest and from it are derived many well-known and valuable plants, among them being *Fritillaria imperialis*, *Hyssopus officinalis*, *Jasminum officinale*, *Nepeta Mussinii*, *Papaver orientale*, *Philadelphus coronarius*, *Platanus orientalis*, *Prunus communis*, *Spinacia oleracea* and *Tupila Gesneriana*. It seems fairly certain too that barley (*Hordeum vulgare*) and at least some kinds of wheat (*Triticum* spp.) originated here.

From the great desert and semi-desert areas which form the eastern part of the region come such familiar or characteristic plants as *Astragalus Tragacantha*, *Iris halophila*, *Lonicera persica*, *Polygonum Baldschuanicum*, *Rheum Rhaponticum* and *Limonium* (*Statice*) *Suworowii*.

Where, as is often the case, the deserts are saline, halophytes like *Haloxylon Ammodendron* and *Salsola arbuscula* are conspicuous.

The Tibetan plateau proper forms a rather specialised area chiefly on account of its great elevation (141). Here *Poa altaica* has been recorded from a height of 19,000 ft., and among other noteworthy species are *Caragana versicolor*, *Kobresia tibetica*, *Myricaria prostrata* and *Primula Florindae*.

Mediterranean Region

Perhaps the most outstanding feature of plant distribution in this region is the way in which many of the species (just as do many of the genera) extend out of the region proper far up the western coasts of Europe, often reaching even to the British Isles.

Apart from this, however, the flora is well defined, except perhaps in Asia Minor, and, owing to the marked geography of the region, can be divided up into a number of parts.

It is a very rich flora with considerable endemism and, taking into account that

the Mediterranean has been the cradle of many human civilisations, it is not surprising to find that the native plants of it have contributed largely to both horticulture and agriculture. The type of vegetation prevailing over much of the region is the very characteristic "maquis" or thicket, and many of its constituent species, though not of great value, are nevertheless familiar.

The gardeners' debt to the region is well shown by the following, all of which are derived thence: *Anemone coronaria*, *Aubrietia deltoidea*, *Cercis Siliquastrum*, *Chrysanthemum coronarium*, *Cyclamen indicum*, *Hyacinthus orientalis*, *Iris susiana*, *Lavandula Spica*, *Lilium candidum*, *Lilium chalconicum*, *Malope trifida*, *Narcissus Jonquilla*, *Nerium Oleander*, *Nigella damascena*, *Paeonia officinalis*, *Prunus Lauro cerasus*, *Pyracantha coccinea*, *Quercus Ilex*, *Reseda odorata*, *Senecio Cineraria* and *Viburnum Tinus*.

Economic plants include *Allium Porrum*, *Capparis spinosa*, *Cynara Scolymus*, *Ficus Carica*, *Laurus nobilis*, *Mandragora officinarum*, *Olea europaea*, *Petroselinum crispum*, *Quercus Suber* and *Scolymus hispanicus*.

In addition to the endemics of the littoral areas almost every island has its own peculiar species; Corsica and Sardinia, for instance, are said to have about fifty each.

Among the constituent parts of the region the Atlas Mountains are of special interest. Their flora is still by far the least completely known and has many very interesting features. It has been suggested, for instance (154), that it represents to a considerable extent a remnant of the old north temperate flora of the Tertiary epoch which has found there a refuge where it has survived the effects of the Pleistocene glaciation, in much the same way as a vastly greater part of the old flora survived in the mountainous parts of the Sino-Japanese region.

Macaronesian Transition Region

In an insular region of very small total land area such as this the question of the proportion of species endemism is particularly illuminating, but unfortunately the figures are not easy to obtain because the islands have so long felt the influence of man that it is often almost impossible to separate the alien from the native plants.

In the Azores Guppy (108) estimates that the forty or so endemic species represent a proportion of some 20 per cent. of the native species. The flora is essentially the remnant of a forest flora and its general affinities are with western Europe. Among the endemic species are *Campanula Vidalii*, *Erica azorica* and *Vaccinium cylindraceum*.

Madeira has about 100 endemics and perhaps the proportion is roughly the same as in the Azores. The flora again is a forest flora and closely related to the Mediterranean flora. Cockerell (46) has pointed out that the endemic species are chiefly of two kinds, either isolated, or closely related to European forms. Among the former are *Clethra arborea* and *Pittosporum coriaceum*, and among the latter *Sambucus maderensis* and *Sorbus maderensis*.

The Canary flora, again, is a forest flora and chiefly related to that of North Africa. Its endemics have been estimated at about 400, and this is certainly a higher proportion than either of the above.

A number of the native species are fairly familiar either in gardens or as specially characteristic of the vegetation, these including *Canarina canariensis*, *Dracaena Draco*, *Kleinia neriifolia*, *Periploca laevigata*, *Semele androgyna*, *Sempervivum spathulatum*, *Tamus edulis* and *Viburnum rugosum*.

One of the noteworthy features of the flora is the great development of succulent members of the Crassulaceae and especially the genus *Sempervivum*. These species afford a most interesting study in segregation and endemism, and an excellent account of them has been given by Præger (185).

The flora of the Cape Verdes has been much less studied than that of Madeira or the Canaries, and it is difficult to say what proportion the sixty-odd endemic species represent. The affinities of the flora are with adjacent Africa, as is instanced by *Lavandula rotundifolia* and *Campanula Jacobaea*.

Among species linking the islands together or with the Eur-African continent may be mentioned *Laurus canariensis* and *Myrica Faya*, which occur on the Azores, Madeira and the Canaries; *Cistus monspeliensis* on the Canaries and in the Mediterranean; *Centranthus Calcitrapa* on Madeira and the Canaries; and *Ruscus hypophyllus*, which ranges from Madeira to the Caucasus. In the last-named the Madeiran plant has been described as a separate species.

Atlantic North American Region (288)

In so large an area as is covered by this region the proportion of endemic species is naturally high, but the main feature of the flora is almost certainly its general resemblance to that of temperate Eurasia. For instance, many species of the Old World are represented in the New World by others very closely related to them, and many of these afford excellent examples of species-pairs, a subject which will be discussed at greater length in the next chapter.

Eastern North America has not contributed many plants of economic value to the common store, and such as there are are for the most part drug plants like *Hamamelis virginiana*, *Hydrastis canadensis*, *Lobelia inflata*, *Podophyllum peltatum*, *Polygala Senega* and *Ulmus fulva*, although the sugar maples (*Acer saccharum*, etc.) and the hickories and pecans (*Carya* spp.) must not be forgotten.

As might be expected from the similarity of latitudes, the region has provided a number of important garden plants, among them being *Acer Negundo*, many Michaelmas daisies (*Aster* spp.), *Catalpa bignonioides*, *Cornus florida*, *Juglans nigra*, *Kalmia latifolia*, *Lilium philadelphicum*, *Lobelia cardinalis*, *Magnolia grandiflora*, *Monarda fistulosa*, *Phlox subulata*, *Rhus typhina*, *Robinia Pseudo-acacia* and *Tradescantia virginiana*. The prairies, in particular, have provided a number of Composites, among them *Gaillardia aristata*, *Helenium autumnale* and *Rudbeckia hirta*.

Among other particularly interesting or characteristic plants of eastern North America are *Castilleja coccinea*, *Gaultheria procumbens*, *Gymnocladus canadensis*, *Maclura pomifera* (aurantiaca), *Menispermum canadense*, *Nyssa aquatica*, *Platanus occidentalis*, *Prunus serotina*, *Rhododendron maximum*, *Rhus Toxicodendron* and *Sabal Palmetto*.

The north-east part of the region, round the Gulf of St. Lawrence, has been the scene of some exceptionally interesting studies in plant distribution in recent years.

Fernald (76-79), in particular, has shown that there is in this area a considerable group of plants, many of which are endemic, either identical with or very closely related to plants found elsewhere only in the western North American mountains, or more rarely in parts of continental Asia. Moreover, he shows that these plants have, in north-eastern America, a very local and restricted distribution and are in fact found only on areas (such as the Gaspé Peninsula, western Newfoundland,

the Magdalen Islands and parts of north-east Labrador) which, there is reason to believe, were unglaciated during the Pleistocene. That is to say the plants are restricted to former "nunataks." His explanation of the many curious facts that he describes is that the species concerned lived throughout the Pleistocene in the Arctic, and that during this time they migrated to where they are now found. There they have since persisted and have not, as might otherwise seem possible, been derived by migration eastwards from western North America.

More recently Marie Victorin (159) has also investigated the distribution of plants in this part of the world and has confirmed many of Fernald's observations, but he has also emphasised the great interest of the area from the point of view of plant evolution and species production.

He refers not only to the restricted endemic forms already mentioned but also to the more familiar features exhibited by such genera as *Senecio* and *Crataegus*, which are here represented by such an array of minor species or forms as almost to defy classification. With regard to the latter especially he expresses the interesting opinion that many of these forms have originated as a result of deforestation and human settlement. They are, therefore, to be regarded as very young species, and it follows, moreover, that in certain circumstances forms of this kind may be produced in two or three hundred years, which is, of course, the period of European settlement in North America.

He also draws attention to the fact that many of the local endemics are found only in estuarine conditions, and that sometimes the local segregation of forms in these conditions is most marked, as, for instance, in *Bidens hyperborea*, and adds something to Fernald's conceptions by recognising certain endemic species as having persisted during glaciation on nunataks, but as having migrated slightly from those areas since.

His general conclusions are, first, that the floras of western and eastern North America were long separated by an arm of the sea; second, that eastern North America has become gradually isolated from Europe by geographical changes; and third, that the flora of north-eastern North America has evolved chiefly in response to two more recent factors, namely glaciation and the widespread occurrence of estuarine conditions, both of which have amounted to physiological isolation.

Pacific North American Region

Like the last this region has not contributed much in economic plants, but garden species originating here are very numerous and include *Arbutus Menziesii*, *Ceanothus thyrsiflorus*, *Clarkia elegans*, *Cornus Nuttallii*, *Eschscholzia californica*, *Garrya elliptica*, *Gaultheria Shallon*, *Godetia* spp., *Lupinus arboreus*, *L. polyphyllus*, *Mahonia Aquifolium*, *Mimulus moschatus*, *Nemophila Menziesii*, *Phacelia* spp., *Ribes aureum* and *Tolmiea Menziesii*.

By far the best-marked constituent flora of the region, and in many ways the most interesting, is that of California, which is a good example of "Mediterranean" flora, that is to say one showing the same peculiar type of vegetation (evergreen thicket or scrub) as is seen in that of the Mediterranean region itself. The Californian flora like all "Mediterranean" floras has a high proportion of endemism and considerable richness, and a good account of it and its affinities has been given by Abrams (1).

Among characteristic species of this part of western North America may be

mentioned *Artemisia tridentata*, *Erythronium grandiflorum*, *Fouquieria splendens*, *Lewisia rediviva*, *Penstemon heterophyllus*, *Quercus chrysolepis*, *Rhododendron californicum* and *Washingtonia filifera*.

Well-known species from the more northerly part of the region include *Aquilegia formosa*, *Lupinus nootkatensis* and *Rosa nutkana*.

North African—Indian Desert Region

As is to be expected from the nature of the terrain, the flora of this large region is comparatively poor and very specialised. It includes one very important economic plant, *Phoenix dactylifera* (the date palm), and a few minor ones like *Boswellia Carteri* and *Balsamodendron Myrrha*, and various species of *Acacia*, but rather naturally no garden plants.

Although a good many of the species are widespread, as, for example, *Calotropis procera* and *Lawsonia inermis*, the majority are more or less confined to one of the three main constituent areas: the Sahara; Arabia and Mesopotamia; north-west India.

Instances of the first of these are *Anabasis aretioides*, *Anastatica hierocuntica*, *Aristida pungens*, *Asteriscus pygmaeus*, *Calligonum comosum*, *Farsetia aegyptiaca*, *Limoniastrum Guyonianum*, *Retama Rhaetam* and *Salvadora persica*.

The second includes *Balsamodendron Opobalsamum* and *Catha edulis*, and the third *Prunus Mahaleb* and *Quercus infectoria*.

Sudanese Park Steppe Region

Although this region is a large one its flora is neither particularly rich nor of any special interest. The vegetation throughout it is some kind of savannah or park-land, and such is not usually very rich in species. It is a region of open spaces and is far better known for its fauna, which is or was extraordinarily abundant, than for its plants.

In one sense it may be considered as a westerly extension of the East African steppes with which it encircles the forests of the Congo and Niger, and its strongest floristic affinities are in this direction.

Species of *Acacia*, grasses and palms are among the most conspicuous of its plants, and instances of these are included in the following list of species more or less characteristic of the region as a whole, namely *Acacia Senegal*, *Andropogon Gayanus*, *Borassus aethiopicum*, *Cassia Senna*, *Cola acuminata*, *Entada sudanica*, *Hyphaene thebaica*, *Kigelia aethiopica*, *Loranthus Acaciae*, *Phoenix reclinata* and *Themeda triandra*.

North-east African Highland and Steppe Region

Abyssinia, which comprises by far the larger part of this region, has a rich and interesting flora and one that is of special theoretical importance in regard to the development of the tropical African montane flora in general. It is as yet not very completely known, but it can be said that in addition to a considerable element of tropical African affinity it also contains a considerable number of types more characteristic of the northern temperate regions.

In *Coffea arabica* it has provided at least one economic plant of first importance,

but apart from this its species are not very familiar or important. Among those particularly characteristic of the area may be mentioned *Acacia abyssinica*, *Aloe abyssinica*, *Eragrostis Tef* and *Euphorbia abyssinica*.

The remainder of the region is, for the most part, of less interest and its flora is a depauperate one chiefly of African affinity, containing no plants of special note.

Socotra, however, has a very interesting flora with, considering its slight degree of isolation, a marked amount of endemism (83). The first comprehensive account of it is that of Balfour (11), who visited the island in the eighteen-eighties. To-day it is known to possess about 200 endemic species representing a proportion of about 40 per cent.

West African Rain-forest Region

This region, which corresponds, as the only equatorial forest zone in Africa, to the whole of the Amazon region or of Monsoon Asia, has a very rich flora which is still far from completely known, but, as might be expected, it has not yet at any rate provided many useful plants, as far as world commerce is concerned. On the other hand, quite a number of indigenous species have been exploited by the native peoples and, in addition, the flora contains a number of valuable timber trees.

Among the economic plants two, *Coffea liberica* and *Elaeis guineensis*, are of outstanding importance, and others with a more local value include *Aframomum Melegueta*, *Raphia vinifera*, and the native rubber plants, *Funtumia elastica* and *Landolphia owariensis*. Among timber trees, *Khaya senegalensis*, *Piptadenia africana* and *Staudtia gabonensis* may be mentioned.

Other species characteristic of the region are *Clerodendrum splendens*, *Erythrina excelsa*, *Monodora Myristica*, *Spathodea campanulata* and *Strophanthus hispidus*.

The islands of the Gulf of Guinea have a considerable proportion of endemic species (281). They are mostly mountainous and the floras show some affinity with the other tropical African mountains, but they also possess many species such as *Abutilon grandiflorum*, *Costus giganteus* and *Xylopia aethiopica* which link them up with the continent in general.

East African Steppe Region

The typical vegetation of this great region is savannah, but in the highlands and in the south-eastern part forests are well developed and altogether there is considerable heterogeneity, and the area can be and has been divided up floristically in great detail. Despite this, few of the native plants are familiar, and there are practically no economic plants of importance except a few timber trees such as *Berlinia Baumii*, *Burkea africana* and *Pterocarpus erinaceus*.

The flora of the eastern highlands is discussed at some length below, and apart from this the flora of the region as a whole tends to divide into western and eastern parts, the former comprising Angola and Rhodesia and the latter Portuguese and British East Africa. Among characteristic species of the former are *Brachystegia* spp., *Clematis Welwitschii* and *Ziziphus mucronata*, while those of the latter include *Arundinaria alpina*, *Hagenia abyssinica*, *Hypericum lanceolatum*, *Musa Holstii* and *Olea chrysophylla*.

The Flora of the Tropical African Mountains

It was seen in an earlier chapter that high mountains are by no means confined to the temperate regions of the world and that there are in fact elevations so great that their summits bear perpetual ice and snow in all continents and at all latitudes. The equatorial mountains, however, are, for the most part, portions of long ranges or systems whose extremities run far into the temperate regions, so that there is little geographical isolation associated with them. This is so, for instance, in the case of the tropical Andes in the New World and in the case of the Malayan mountains which connect up with the essentially temperate Himalayan mass. Only Africa is a marked exception. Here the mountains of the tropics, instead of being parts of a continuous zone, are isolated masses, so separated from one another and rising so abruptly out of the lowlands that they have gained for themselves the geographical term of "Inselberge." Each is, as it were, an island of elevation separated not only from its fellows but also, and more so, from any considerable mountain system of the temperate regions.

It is, no doubt, this circumstance that makes the flora of the higher levels of the African equatorial mountains one of the most remarkable and specialised in the whole world. Like other high mountains they have their "alpine flora," but this is very different from anything which corresponds to it elsewhere. Moreover, the difference is one of type as well as degree.

Like other high mountain floras, too, that of tropical Africa consists to a very great extent of genera familiar to everyone in temperate floras and often providing arctic-alpine species, but in Africa not only are the species quite distinct but they have, usually an entirely different kind of growth-form (Plates 8, 13, 14), with the result that the flora in general of the upper levels of these African mountains can only be described as like nothing else on earth and by usual standards extremely bizarre.

This is, no doubt, related to a point which has frequently been made that the montane floras of the tropics generally consist, not of modified species from the lower zones, but of forms obviously related to the floras of more temperate and arctic regions. It is here that the African alpine floras are peculiar, because although there are in them many temperate types, they are for the most part related closely to the plants of the zones below them. The temperate types proper seem, as Taylor (240) has pointed out, to owe their presence to a different combination of circumstances and do not in fact form so definite an altitudinal *stratum* as in other continents. *Sanicula europaea*, for instance, which is a good example of a temperate plant on African mountains, is common often on the lower slopes and is by no means confined to the highest levels.

The mountains having this peculiar form of high alpine flora are widely scattered and fall into three groups, namely, the Abyssinian peaks; the group of east central Africa (Kilimanjaro, Kenya, Elgon, Ruwenzori and their associates); and Cameroon Mountain and Fernando Po. The general appearance of the vegetation has been described so often by travellers, especially in the case of Ruwenzori (133), that we can confine ourselves here to a consideration of some of the more prominent species and types comprising it.

By far the most outstanding and familiar of the African high montane plants are the so-called "tree *Senecios*" and "tree *Lobelias*." Both belong to very widespread genera, but these mountain species have a most peculiar form. The

Senecios have tall branched woody stems and may, according to some authorities, live for as much as 100 years, flowering and fruiting periodically. Their leaves, however, are not small and scattered as in ordinary trees but are large and more or less aggregated at the ends of the axes, and the branching is far less diffuse. These *Senecio* species are entirely confined to the tropical African mountains. The *Lobelias* are what may be called long-term monocarpic plants, that is to say they grow vegetatively for fifteen or twenty years, then flower and die. The word tree as applied to them is simply a rough indication of their unusual size, because in habit they are actually tall and massive unbranched columnar woody herbs. In their most typical form they occur only on the African mountains, but a few similar species are known from Asia. They are also far less rigidly confined to the highest levels than the *Senecios*. It is interesting that the higher the situation of these plants the more restricted is their range, and Taylor has stated that of both genera no species among the highest-zoned is found on both sides of the Great Rift Valley. It is this very remarkable degree of segregation between the mountains that is perhaps the most interesting feature of their geography, and this cannot be better illustrated concisely than by quoting, in somewhat broadened form, a table given by Bruce (32).

Distribution of the Giant Lobelias on the mountains of Tropical Africa

[illegible]

The giant *Senecios* are more restricted in that they do not occur on the western mountain group. According to Cotton (49) there are 17 species, all peculiar to one mountain or group, namely, 4 on Ruwenzori ; 3 on Kenya ; 2 on the Aberdares ; 2 on the Virungas ; 3 on Elgon ; and 3 on Kilimanjaro.

The African high montane representatives of several other genera also have been revised (84, 85), with the following statistical results.

Anagallis has 15 species, mostly like *A. tenella* in appearance, and there are local species on most of the eastern mountains and in Abyssinia.

Swertia, of interest as a close relative of *Gentiana*, has 30 species : 8 in Abyssinia and the rest on the eastern mountain group.

Echinops has 9 species : 2 from Abyssinia and 7 from the eastern mountains.

Sonchus has 27 tropical and South African species, and several are on the eastern mountains.

Bartsia has 11 species : 3 in Abyssinia, 1 in Abyssinia and the eastern mountains, 6 on the eastern mountains, and 1 on Cameroon Mountain.

Veronica has 11 species : 1 in Abyssinia and the eastern mountains, 9 on the eastern mountains, and 1 on Fernando Po and Cameroon Mountain.

Carduus has 16 species, all on the eastern mountains and showing a high degree of segregation. *Alchemilla* and *Hypericum* are other genera which contribute characteristic forms to the general montane flora.

A particularly interesting and characteristic element in the African montane flora is afforded by the members of the tribe Ericaceae of the Ericaceae, and these plants have also been monographed (86, 87). *Erica* itself has 15 species in tropical Africa, including the widespread *E. arborea*, but most of them are from the south-east and few of them are really montane. In connection with their mention here it is interesting to observe that Chevalier (42) concludes that the genus originated in tropical Africa and is a relic of the old xeromorphic Tertiary flora of that region.

The genus *Blaeria* is actually discontinuous, because it occurs on the Cameroon Mountain and Fernando Po. It has in all 21 tropical species in a special section (the others are at the Cape), and of these all but two are montane. Of the two species mentioned in West Africa, one, *B. tenuifolia*, is also on the Aberdares.

Philippia has 40 species distributed widely in the tropics and in Madagascar, etc. Of the tropical African species four are on the eastern mountains, one of them, *P. excelsa*, being on several peaks, and there are two species on the western mountains.

East African Island Region

In general the flora of Madagascar and its neighbouring islands may be described as of African affinity with a strong Asiatic element.

This is seen well in Madagascar itself. The proportion of endemic species is high, perhaps as much as 75 per cent., but most of them are related to African species and, in addition, there are about twice as many species common to the island and to Africa as there are common to the island and Asia. There are also said to be points of resemblance between the flora of some of the more elevated parts of Madagascar and that of the East African mountains.

Madagascar has few economic or horticultural plants, and all that can usefully be done is to list some of the more familiar or characteristic, one or two of which are occasionally cultivated. Among these are *Angraecum sesquipedale*,

Aponogeton fenestralis, *Euphorbia fulgens*, *Raphia Ruffia*, *Ravenala madagascariensis* and *Stephanotis floribunda*.

In Mauritius and in Réunion specific endemism appears to be about 50 per cent., and in the Seychelles it is about 15 per cent.

Region of Ascension and St. Helena

Ascension Island had apparently, when first discovered, no vegetation except on the summit of Green Mountain, and even to-day is said to have only some eight indigenous species, of which at least two, *Euphorbia organoides* and *Hedyotis adscensionis*, are endemic. *Wahlenbergia linifolia* occurs also on St. Helena.

To-day St. Helena has but the vestiges of the rich vegetation which it formerly possessed, and it is therefore difficult to arrive at any satisfactory statistics about its plants. Early visitors describe the island as covered with dense forests right down to the water's edge, but these same visitors left behind them asses, pigs and goats, and the last-named in particular have gradually devastated the original vegetation until to-day almost nothing remains.

Melliss (168) gives a good account of the flora as it was in the eighteen-seventies. He enumerates some 900 species of flowering plants as occurring on the island, but considers only about 30 of them to be really native, all the rest being under suspicion of accidental or deliberate introduction. Of these 30 all but two or three are endemic. Some were even at that time very rare if not actually extinct, and the position is worse to-day.

On all counts it seems safe to assume that the aboriginal flora of the island was not large in number of species but very remarkable in being almost entirely endemic.

South African Transition Region

The continent of Africa is unique in that it lies almost symmetrically astride the equator. It is true that owing to the actual shape of the continent the northern part is much larger than the southern, but in latitudinal extent there is little difference between them and in both hemispheres the continent stretches into extra-tropical regions. The plant life of Africa as a whole thus comes to include three perfectly distinct floras—a warm temperate northern, a tropical central or equatorial, and a warm temperate southern. At the same time the first and last of these are of that peculiar type known as “Mediterranean,” and are not only rich but to a considerable extent specialised floristically.

It might be expected therefore that the flora of tropical Africa would show and include appreciable elements from these floras, and that there would be conspicuous zones of mingling or transition. In fact this is much less than might be anticipated, for the reason that on the equator side of each of the “Mediterranean” floras the climate is such as to produce desert conditions. In the north this desert belt—the Sahara—is so complete that there is no transition zone between the Mediterranean flora and the tropical African flora at all, but in the south conditions are not so extreme. The deserts there are more scattered and less arid on the whole, and along the east coast the climate is so favourable as to support the development of forest.

As a result of these circumstances there is, in southern Africa, what is not found in the north, namely a very important transition floristic region where the tropical

African flora and the southern "Mediterranean" flora, the Cape flora, mingle (2, 22). This transition region is of considerable size, but its flora is not very rich and is of interest chiefly in the way in which it illustrates (perhaps as well as any other flora in the world) how two floras may by mutual intermigration weld themselves into a kind of hybrid whole.

The South African transition region is, as has been suggested, easily divisible into a number of parts, and as here floristic and geographic distinction goes hand in hand, it is appropriate to consider what these are. The main constituent areas and floras are four in number—the high veldt of the Transvaal and Orange Free State; the Kalahari desert or semi-desert of Bechuanaland; the desert or semi-desert of South West Africa; and, to the south, the desert of the Karroo.

Such is the usual classification of the region, and it will be noticed that it does not include the eastern coastal forest region. This has already been dealt with incidentally, because on account of the great preponderance of tropical types in its flora it is more generally considered to form a south-easterly extension of the East African steppe region. This treatment is actually a rather arbitrary one, because in its most southerly parts at least this area shows a marked mingling of tropical and southern types, but the simplest course is to adhere to it here.

As is only to be expected, this region has not contributed much either to gardens or to economic botany, and the importance of its flora lies in more scientific and academic directions. On this account it is enough to mention a few of the more conspicuous and characteristic plants.

Of the four areas mentioned above the first three show comparatively little difference in vegetation and may here be considered together. Among the noteworthy members of their vegetation are *Acacia Giraffae*, *Acanthosicyos horrida*, *Carissa Arduina*, *Dioscorea elephantipes*, *Elephantorrhiza Burchellii*, *Euphorbia tetragona*, *Rhigozum trichotomum* and *Sarcocaulon Patersonii*.

The flora of the Karroo is much more specialised and indeed is one of the most striking examples of a xeromorphic flora in the world, a conspicuous feature of it being the "stone plants" (160) belonging to *Lithops* and other genera (Plate 11), so called from their great resemblance to the pebbles of the deserts in which they grow. The Karroo plants, which include also many species of *Mesembryanthemum* and related genera, *Crassula falcata*, *Crassula lycopodioides*, *Senecio articulatus*, *Rochea coccinea*, many Stapeliads, and species of *Gasteria* and *Haworthia*, are becoming increasingly familiar to-day because there is a fashion for their cultivation, and it is worth while reminding readers that the flora also includes quite other kinds of plants, such as *Acacia Karroo*, *Chrysocoma tenuifolia*, *Elytropappus rhinocerotis*, *Euclea undulata* and *Euryops tenuissima*.

The Cape Region

The area occupied by the Cape flora proper, which, as we have already seen, is one of the most remarkable in the world, is very small, consisting, roughly speaking, of the coast zone from Clanwilliam on the west to the neighbourhood of Port Elizabeth on the east. At the same time it is probably in proportion to its size the richest flora in the world. It is not easy to arrive at statistics of the region as a whole, because it does not fit in with any political area, but some measure of its richness may be gained from the fact that the Cape Peninsula itself, which is little bigger than the county of Rutland, possesses in all 2,500 species, 750 of which are Monocotyledons.

The Cape flora has few plants of economic importance, partly no doubt because the region had, before its European colonisation, a very sparse and primitive human population, and the only ones which need be mentioned are one or two timber trees, including *Ocotea bullata* and *Olea verrucosa*, which come from the eastern part of the region, where true forest is developed.

This lack of economic plants is more than balanced by the great numbers of garden plants which the Cape has provided, and the botanical exploration of this country was a horticultural occasion of first-class importance, as the following list will show :

Agapanthus africanus, *Amaryllis Bella-donna*, *Arctotis stoechadifolia*, *Asparagus plumosus*, *Dimorphotheca* spp., innumerable species of *Erica*, *Freesia refracta*, *Galtonia candicans*, *Gazania* spp., *Gerbera Jamesoni*, *Gladiolus* spp., species of *Ixia* and *Kniphofia*, *Lobelia Erinus*, *Nemesia* spp., *Pelargonium acerifolium* etc.

It may also be noted that one of the commonest of all garden plants, *Montbretia*, whose proper name appears to be *Crocasmia crocosmiaeflora*, is an artificial hybrid between two wild South African plants.

Besides these there are many other native plants which, although not generally cultivated, are nevertheless more or less familiar, and among them may be mentioned :

Brabejum stellatifolium, *Disa grandiflora*, *Eriocephalus umbellatus*, *Helichrysum vestitum*, *Leucadendron argenteum*, *Leucospermum conocarpum*, *Metalasia muricata*, *Mimetes lysigera*, *Priestleya villosa*, *Protea grandiflora*, *Protea mellifera*, *Rhus tomentosa*, *Satyrium carneum* and *Watsonia rosea*.

Indian Region

Geographically, and in other ways too, India is a well-defined area and it has a rich and characteristic flora, whose chief relationship is with that of south-east Asia and the Malayan Archipelago.

It contains many plants of value, among useful plants which appear to be native here being *Aegle marmelos*, *Artocarpus nobilis*, *Corchorus capsularis*, *Crotalaria juncea*, *Elettaria repens* (*Cardamomum*), *Eleusine coracana*, *Indigofera tinctoria*, *Luffa aegyptiaca*, *Murraya Koenigii*, *Pennisetum glaucum*, *Piper longum*, *Piper nigrum*, *Pterocarpus santalinus* and *Sesamum indicum*.

A few of its species, including *Cymbidium grandiflorum*, *Datura Metel*, *Dendrobium nobile*, *Hibiscus Abelmoschus*, *Jasminum grandiflorum*, *Vanda caerulea* and *Vitex Negundo*, are sometimes grown in hothouses, and among other interesting plants there may be mentioned *Bombax malabaricum*, *Butea frondosa*, *Calotropis gigantea*, *Corypha umbraculifera*, *Dorstenia indica*, *Ficus bengalensis*, *Ficus elastica* and *Shorea robusta*.

Naturally there is a high degree of community between the floras of India and Ceylon, and many species, as for instance three of the large Asiatic *Lobelias*, *L. Leschenaultii*, *L. nicotianifolia* and *L. trichandra*, are found in both, as well as some of those already mentioned.

The flora of Ceylon is more strongly Malayan in affinity than Indian and it has a high degree of endemism. Willis (262), who has studied the flora in great detail in connection with his theory of Age and Area, estimates that there are over 800 endemics and that these form about one-third of the whole native flora.

Most of the better-known plants of Ceylon are found either in India or elsewhere also, but among endemics *Diospyros Ebenum* (the ebony), *Diospyros quae-sita*, *Hortonia angustifolia* and *Schumacheria castaneifolia* merit mention.

Continental South-east Asiatic Region

This region can be dealt with fairly shortly here for several reasons. It is certainly one of the least individual of the regions and, although it is in general convenient to treat it as a separate entity, its flora is essentially part of the great Malayan flora and is scarcely separable from that of the Malayan Archipelago next to be mentioned. Again, the flora of much of the region, although rich, is relatively little known and there are few really familiar plants which are not found elsewhere also.

Among species particularly associated with the region there may be mentioned *Amherstia nobilis*, *Cinnamomum Camphora*, *Dipterocarpus turbinatus*, *Garcinia cochinchinensis*, *Liquidambar formosana* and *Melanorrhaea usitata*, but it is in connection with certain outstanding economic plants that this part of the world deserves special notice.

Attention has already been called to the fact that it is often now extremely difficult to say for certain where important crop plants had their original home. This applies amongst others to rice, tea and the various members of the genus *Citrus*. To-day these plants are grown widely, but such evidence as there is goes to show that most, if not all of them, were natives of this continental part of south-east Asia, or at least of it and of certain of its bordering lands.

Region of the Malayan Archipelago

Probably nowhere else in the world does flowering plant vegetation attain such a richness and luxuriance as in the Malayan Archipelago, where in almost every way the conditions favour its optimum development (see frontispiece).

Not only is the vegetation luxuriant, but the flora is very rich and contains many plants which have long been of value to man. Indeed, the "Spice Islands," as part of the Archipelago was called in earlier days, have played no small part in the history of many nations (97). The nature of most of these economic plants is indicated by the name just quoted, but there are others as well, and as instances of the products of the region there may be mentioned, all of which are known or thought to have originated somewhere in the Archipelago, *Arenga saccharifera*, *Artocarpus communis* (*incisa*), *Calamus Draco*, *Canarium luzonicum*, *Colocasia esculenta*, *Curcuma Zedoaria*, *Eugenia caryophyllata*, *Garcinia Mangostana*, *Metroxylon Rumphii*, *Musa textilis*, *Myristica fragrans*, *Piper Betle* and *Zingiber officinale*.

Besides these the flora includes innumerable other noteworthy plants, a few of which are occasionally cultivated, among them being *Amorphophallus Titanum*, *Antiaris toxicaria*, *Bulbophyllum grandiflorum*, *Coleus Blumei*, *Croton lacciferus*, *Dendrobium superbum*, *Dendrocalamus giganteus*, *Dryobalanops aromatica*, *Primula imperialis*, *Rafflesia Arnoldi*, *Strychnos Ignatii* and *Vanda tricolor*.

Almost every island shows a considerable degree of specific endemism (144), but the highest number and proportion are found in New Guinea, which has the most interesting and most peculiar flora of all (58). No complete estimate is available, but in a list comprising fifty-three of the native families 85 per cent. of

the species are endemic. The peculiarity of the very rich orchid flora is specially striking, there being something like 2,500 species, practically all of which are confined to the island. New Guinea is a specially important area in plant geography, and the useful accounts of its plant life by Lam (145) and Lauterbach (146) deserve study.

Borneo has about 50 per cent. of endemic species, and the Philippines rather less. The flora of the latter more especially, which includes over a thousand species of orchids, has been much studied in recent years and well described by Merrill (169).

Space will not permit reference to other individual islands, but it may be assumed that all contain many endemics and, moreover, that there is every type of distribution over the different islands, such ranges often being more or less discontinuous. To give but a single instance of this, *Gunnera macrophylla* is said to occur in Sumatra and New Guinea.

The montane flora of the great chain of mountains that runs from end to end of the Archipelago is a subject of great interest which has recently received exhaustive treatment from Van Steenis (249). Here it can only be noted that there appear to have been three principal tracks by which the temperate genera so conspicuous in this flora have migrated into the Archipelago.

One is by the route Malay Peninsula, Sumatra, Java and the Lesser Sunda Islands; another by the line Formosa, Philippines, north Celebes; and the third from Australia by way of New Guinea, Celebes, Borneo and the Philippines. According to Van Steenis about 800 species constitute the "Malaysian Mountain Flora," and this he estimates as 4 per cent. of the whole Malaysian flora, which includes also the Malay Peninsula, which in our classification is included in the last region.

Hawaiian Region

Geographically this is the most isolated of all the floristic regions, a fact which undoubtedly accounts largely for its most remarkable botanical feature, the extreme and intense endemism of its flora. Numerical estimates vary somewhat, but there is reason to believe that of the native plants 85 per cent. may be endemic to the islands, and these are mostly of very marked and specialised types.

Several good general accounts of the plant life (35, 151, 205) mention many of the most characteristic species, such as *Acacia Koa*, *Dianella odorata*, *Edwardsia grandiflora*, *Eugenia malaccensis*, *Gunnera petaloides*, *Santalum pyrularium* and *Strongylodon lucidum*, but there are no noteworthy economic or horticultural plants.

The affinity of the flora to-day is more with America than with Asia, but this is not generally accepted as indicating its origin. Indeed, the problem of the origin of the Hawaiian flora is one of the most difficult in plant geography. Skottsberg (225, 227, 231), who has studied the question in great detail, suggests that the flora is a relic of a very old "Pacific" flora, which now by various geographical and other changes has largely disappeared, and he emphasises the undoubted relation which exists between the floras of Hawaii and of Juan Fernandez. One point of difficulty in this view is that the Hawaiian islands are comparatively recent volcanic islands. Another view is that the flora originated chiefly from Central America. Finally there are others who believe in a "waif and stray" origin, namely that the flora has developed from a heterogeneous collection of plants which have reached the islands by all sorts of casual means.



Plate 14. A Giant Senecio (*S. keniodenuron*) of the African Mountains

(from Karsten & Schenck, *Vegetationsbilder*)

Region of New Caledonia

The main constituent part of this region, New Caledonia, an island not very much larger than the county of Yorkshire, in some respects exceeds the Hawaiian islands in the peculiarity of its flora and may perhaps claim to be the most extraordinary in the world. It is a very rich flora of some 3,000 species (a figure about a quarter of that for the whole of Australia), and of these at least 80 per cent. seem to be endemic, including some important whole groups. The island is still comparatively little known and may still yield surprises, but its flora has, according to Guillaumin (105), a more or less equal affinity with Australia and eastern Malaya, a rather smaller one with the Pacific Islands, and a slight relationship with New Zealand. It is worth noting that in it the Composites occupy a surprisingly small place, and that the *Rubiaceae*, *Myrtaceae*, *Orchidaceae* and *Araliaceae* are specially conspicuous.

Schlechter (209) has given a useful account of the vegetation, and the reader may be referred to this for details of species, none of which is particularly familiar or of world-wide importance.

The floras of the Lord Howe (118) and Norfolk Islands are naturally very small and show about 25 per cent. of specific endemism. Several of the most noteworthy plants have already been mentioned or will be referred to elsewhere.

Regions of Melanesia and Micronesia and of Polynesia

For immediate purposes it is convenient to combine these two regions and to restrict comment on them to a few leading statements, because to go into greater detail would tend to obscure what, in a very general survey, is the main characteristic of their flora, namely that it is essentially a derived one, almost entirely Malayan and Australian in affinity.

Indeed in comparison with other parts of the world it is no exaggeration to say that there is no real "Polynesian" flora at all but that the plants of this great area are derived from adjacent floras. Certainly it is as derived that the flora is chiefly to be regarded.

This is not to say there is not a considerable amount of endemism in different islands, especially of course the larger ones. From the figures collected together by Guillaumin (105) and others it would seem that Fiji has the highest proportion, about 50 per cent. Tahiti has perhaps 35 per cent. and Samoa rather less. The other main groups seem all to have figures ranging round 25 per cent.

There are no very familiar or important plants peculiar to these two regions.

Caribbean Region

This is one of the most important regions, not only in the richness and luxuriance of its vegetation, but also because of the large number of valuable plants it has provided, and in these respects it may appropriately be regarded as the New World counterpart of the Malayan Archipelago. Geographically it is rather different, since it consists partly of an archipelago (the West Indies) and partly of a portion of the American continent (Mexico and Central America), and climatically also it is less constant, Mexico in particular having extensive desert areas.

It is not easy to say much about the degree of endemism in the flora of the region as a whole, but Willis (262) has stated that the continental part has 8,000 endemic

species, a figure which certainly represents a very high proportion. Cuba is generally credited with one of the richest floras in the world, and here also, as in other islands of the West Indies, the endemism is undoubtedly high.

Many species are common to both the constituent parts of the region, and among them are *Bletia purpurea*, *Calanthe mexicana*, *Epidendrum polybulbon*, *Prioria Copaifera* and *Swartzia simplex*, but most of the more noteworthy plants either occur beyond the confines of the region or are confined to one or other part of it.

Central America in the wide sense has provided a number of economic plants (one very important), namely *Castilla elastica*, *Haematoxylum campechianum*, *Monstera deliciosa*, *Phaseolus multiflorus*, *Smilax medica*, *Vanilla planifolia* and *Zea Mays*, but its contribution to gardens has been even greater and includes such well-known plants as *Ceanothus caeruleus*, *Choisya ternata*, *Cosmos bipinnatus*, *Dahlia pinnata* (variabilis), *Echeveria* spp., *Euphorbia pulcherrima*, *Lycaste Skinneri*, *Polianthes tuberosa* (actually not known wild but belonging to a Mexican genus), *Salvia fulgens*, *Tagetes erecta*, *Tagetes patula*, *Tigridia Pavonia*, *Zebrina pendula* and *Zinnia elegans*.

Other outstanding plants from this area include *Achras Zapota*, *Cereus giganteus*, *Cordia Gerascanthus*, *Deherainia smaragdina*, *Larrea mexicana*, *Persea americana*, *Plumeria acutifolia* and *Theobroma pentagona*.

The West Indies, on the other hand, have contributed comparatively little to gardens but are the home of many well-known plants of value, most of them tropical fruits, of necessity not very familiar in Europe but nevertheless of great importance in warmer countries. The actual home of many of these is lost, but generally credited with a West Indian origin are *Annona muricata*, *A. reticulata*, *Croton Cascarilla*, *Grias cauliflora*, *Lagetta Lagetto*, *Pimenta officinalis*, *Sapindus Saponaria* and *Spondias Mombin* (lutea).

Besides these there are many other conspicuous species in the flora, as, for instance, *Myrica cerifera*, *Nectandra antillana*, *Ocotea Leucoxylon*, *Pereskia aculeata* and *Sloanea jamaicensis*.

The Bermudas have a small flora of about 150 native species and of these some 8 per cent. are endemic.

Region of Venezuela and Guiana

The flora of this region still needs a good deal of study and it is almost impossible to say what degree of endemism it possesses. Probably it is high, despite the close relationship of the flora to surrounding regions.

The region produces no very conspicuously important or valuable plants, and it must suffice here to mention among characteristic species of the vegetation, many of which are grasses or palms, *Arthrostylidium Schomburgkii*, *Aulonemia Quexo*, *Brosimum Galactodendron*, *Caryocar villosum*, *Copernicia* spp., *Curatella americana*, *Cusparia febrifuga*, *Dipteryx odorata*, *Duguetia quitarensis*, *Mauritia* spp. and *Paullinia Cupana*.

Brazilian Region

Like its Old World counterpart, the Congo forests, Brazil has a very rich flora but one which has been little exploited by man, except in upland regions of the east. There are, however, a number of plants of considerable and, in a few cases, of

outstanding economic importance which are regarded as having their origin here. They include *Ananas comosus* (sativa), *Arachis hypogaea*, *Cephaelis Ipecacuanha*, *Copernicia cerifera*, *Hevea brasiliensis*, *Leopoldinia Piassaba*, *Manihot Glaziovii*, *Nectandra Rodioei*, *Passiflora edulis* and *Quassia amara*.

From the drier parts of the region in the east come several well-known garden plants, including *Begonia semperflorens*, *Bougainvillea spectabilis*, *Datura suaveolens*, *Fuchsia coccinea*, *Passiflora caerulea* and *Salvia splendens*.

The region is so large that figures of specific endemism have no meaning, but there are a number of other noteworthy species which may well be recorded here, namely, *Bactris aristata*, *Bauhinia splendens*, *Cattleya labiata*, *Cocos coronata*, *Erythrina crista-galli*, *Euterpe edulis*, *Geonoma macroclona*, *Hancornia speciosa*, *Manicaria saccifera*, *Oncidium papilio* and *Syagrus Mikaniana*.

Andine Region

This very extended region has been divided into a number of subordinate areas and floras, but the constituent parts which call for mention here are five, namely, the montane (tropical in the north), the tropical coast, the temperate coast, the eastern savannahs or puna, and the Galapagos archipelago. The second of these is predominantly a desert area, and the third includes the Chilean "Mediterranean" vegetation and flora.

The region is above all remarkable for the number of its economic plants, which include many of the most important of all. These come chiefly from the more northerly parts of the montane zone and include *Annona Cherimola*, *Ceroxylon andicola*, *Chenopodium Quinoa*, *Cinchona succirubra*, *Erythroxylum Coca*, *Krameria triandra*, *Lycopersicon esculentum*, *Nicotiana Tabacum*, *Phaseolus lunatus*, *Phaseolus vulgaris*, *Quillaja Saponaria*, *Schinus molle* and *Solanum tuberosum*.

The garden plants, which are also very numerous, come naturally from the more temperate parts, especially the southern mountains and the Chilean coasts, but a number have their homes further north. Among the former are *Alstroemeria aurantiaca*, *Berberis Darwinii*, *Calceolaria integrifolia*, *Escallonia micrantha*, *Fuchsia rosea*, *Geum chilense*, *Lapageria rosea*, *Salpiglossis sinuata*, *Schizanthus pinnatus*, *Tropaeolum speciosum* and *Verbena erinoides*; and among the latter, *Buddleja globosa*, *Ercilla volubilis*, *Heliotropium peruvianum*, *Tropaeolum peregrinum* and several orchids.

Other important and interesting species from the northern parts are *Baccharis Tola*, *Espeletia* spp., *Phytelephas macrocarpa*, *Puya Raimondii* (Plate 7) and *Quercus Humboldtiana*, while from the more southerly parts come *Azorella multifida*, *Drimys Winteri*, *Eucryphia cordifolia*, *Gunnera chilensis*, *Jubaea spectabilis*, *Laurelia aromatica* and *Mutisia viciaefolia*.

The Galapagos or Tortoise Islands form a group of volcanic islands about 700 miles west of the coast of Ecuador, and have long been famous for the peculiarities of their animal life. The plant life is not so remarkable, although it contains many points of great interest.

There are nineteen islands varying greatly in size and having a total area rather less than that of Devonshire, and the flora is not rich, amounting to about 350 species. According to Stewart (235), 40 per cent. are endemic, and the families *Amaranthaceae*, *Euphorbiaceae* and *Rubiaceae* are especially rich in endemic forms. The relationship of the non-endemic species is almost entirely American, there being but a very small number of more widely ranging plants.

Kroeber (143) has studied in particular the distribution of the species among the islands, and concludes that there is little in it which cannot be explained on a combination of mathematical and geographical chance.

Pampas Region

This region, which vegetationally is one of the world's most important grasslands, contains no very important economic plants but has provided a small number of garden forms, including *Cortaderia Selloana*, *Nicotiana affinis*, *Petunia* spp. and *Salpichroa rhomboidea*.

Characteristic species include *Aspidosperma Quebracho* and *Trithrinax campestris*.

Region of Juan Fernandez

This small group of three volcanic islands lying off the coast of Chile has a small but peculiar flora.

According to Skottsberg (223, 224, 229), about 70 per cent. of the 142 species are endemic. Rather more than half the flora has a strong American affinity, but the remainder has an equally strong "Pacific," or western, affinity and in particular there is an appreciable relationship with Hawaii.

There is considerable segregation of species between the two large islands, only 19 per cent. of the flora occurring on both. Of endemic species only 12 per cent. occur on both.

The more outstanding species have already been sufficiently indicated in Chapter 7.

North and East Australian Region

This region stretches in a wide coastal belt round the continent from the Kimberley district in the north-west to Tasmania. Vegetationally it is predominantly savannah or savannah-woodland, but there are considerable areas of forest.

The flora is almost entirely local and Australian in character except that in the north there is a considerable admixture of Malayan, and especially New Guinea, forms.

The forest areas contain a number of useful timber trees such as *Castanospermum australe*, *Casuarina torulosa*, *Dysoxylum Fraserianum*, *Elaeocarpus grandis* and *Eucalyptus pilularis*, but otherwise there are no economic plants of note.

A few garden plants are natives of this region, among them being *Acacia dealbata*, *Grevillea robusta*, *Humea elegans*, *Nicotiana suaveolens*, *Trachymene caerulea* and *Viola hederacea*.

The north coast has some 15 per cent. of its species in common with Malaya, and the east coast has a strong relationship with the flora of New Caledonia.

Other notable species of the region are *Alphitonia excelsa*, *Calamus australis*, *Clianthus Dampieri*, *Doryanthes excelsa*, *Drimys lanceolata*, *Eucalyptus marginatus*, *Melaleuca Leucadendron*, *Nothofagus Cunninghamii*, *Olearia nitida*, *Pandanus tectorius* and *Telopea speciosissima*.

South-west Australian Region (295)

Although small this region is floristically a very important one, containing the fifth and last of the world's "Mediterranean" floras. Like the others, and especially like the Cape flora, with which it has many interesting features in common, it is a rich flora showing a very high degree of endemism which may perhaps reach, or even exceed, 75 per cent. Its similarity with the Cape flora lies not so much in the actual number of forms in common, which are indeed few, but in the remarkable degree of parallelism between the leading characters of the two. In both the same families are frequently well developed, and the same types of growth form are common in each.

There are no important economic plants and it is surprising to find, in view of the large number of garden plants which have come from the other "Mediterranean" floras, that the horticultural representatives are also few—so much so that *Brachycome iberidifolia*, *Helichrysum bracteatum* and one or two species of *Helipterum* practically exhaust the list.

The flora contains many very characteristic forms, and among these may be cited many species of *Acacia*, *Banksia*, *Bauhinia*, *Dryandra*, *Eucalyptus* and *Hakea*, *Kingia australis*, *Nuytsia floribunda* and *Xanthorrhoea Preissii*, and many members of the Epacridaceae, Goodeniaceae and Stylidiaceae.

Central Australian Region

The flora of this great area which comprises most of the interior of the continent is comparatively limited, in correlation with the desert or semi-desert conditions which prevail over most of the region. It is also still incompletely known and studied, and it is therefore not possible to say much here about it. It is probably almost entirely endemic.

Among characteristic species, some of which give an important facies to wide areas of vegetation, may be mentioned *Acacia aneura* (mulga), *Acacia harpophylla* (brigalow), *Eucalyptus hemiphloius* (mallee), *Eucalyptus oleosus*, *Melaleuca acuminata* and *Swainsonia Greyana*.

New Zealand Region

The flora of New Zealand (70) must always be of special interest to British botanists because of its antipodal geographical relationship, but comparison of the two is also revealing because, while the British Islands are continental islands, New Zealand is, and has presumably long been, separated from the nearest continent by over 1,000 miles of deep water (177).

The flora of New Zealand is usually estimated at about 1,000 species, but a recent compilation (43) puts the number at 1,850, together with 427 groups of species hybrids and over 600 exotics. Except for the hybrids, which form one of its most remarkable features, the flora may be said to be about the same size as the British, but it differs very markedly because no less than 75 per cent. of its species are endemic and quite unlike those of any other country, while Great Britain has, as we shall see, to all intents and purposes no endemic plants. Of Dicotyledons alone the proportion of endemics is even higher.

Five elements have been recognised in the flora :

1. An ancient palaeozealandic element.
2. An Australian element.
3. A subantarctic element showing a strong relationship with South America.
4. A palaeotropical element.
5. A cosmopolitan element.

Of the non-endemic species 200 are found in common with Australia and 100 with America.

The vegetation is varied but for the most part is some kind of woodland, and there are several valuable timber trees, including *Hoheria populnea*, *Knightia excelsa*, *Metrosideros robusta*, *Nothofagus fusca* and *Plagianthus betulinus*. There is one important economic plant, *Phormium tenax*.

The region has provided several good garden plants, among them *Clianthus puniceus*, *Fuchsia procumbens*, many species of *Hebe*, *Olearia Haastii*, *Olearia paniculata* and *Senecio Greyii*.

Characteristic species include *Aristotelia racemosa*, *Cordyline australis*, *Danthonia pilosa*, *Haastia pulvinata*, *Hebe* spp., *Lagenophora Forsteri*, *Laurelia novae-zealandiae*, *Pittosporum tenuifolium*, *Poa caespitosa*, *Ranunculus Lyallii*, *Rubus australis* and *Weinmannia Tawa*.

The region includes, besides New Zealand proper, four outlying islands or island groups, the Auckland and Campbell Islands on the south, the Chatham Islands 500 miles away to the east, and the Kermadec Islands 600 miles to the north-east. Floristically the last two are the most important, and both have about 15 per cent. of endemic species. The latter (176, 177, 179) has both New Zealand and Pacific floral elements, and the endemics include two species of *Coprosma*.

Patagonian Region

This small region is of special interest because it is the only continental area in the southern hemisphere of latitude similar to that of north and central Europe. It divides up into three constituent areas: the woodlands of the west coast and Fuegia; the southern tip of the Andes and the steppes of south Patagonia; and the Falkland Islands.

The flora is small and none of the species is of value, although a few, like *Pernetia mucronata*, *Philesia buxifolia* and *Oxalis enneaphylla* (Falklands), are sometimes grown in gardens. Its most remarkable feature is its relationship with that of New Zealand.

Among other outstanding species are *Bolax glebaria*, *Empetrum rubrum*, *Gunnera scabra*, *Mulinum spinosum*, *Myrtus nummularia*, *Nothofagus betuloides*, *Nothofagus pumila*, *Opuntia Darwinii* and *Poa flabellata*.

According to Skottsberg (222), the Falklands have about 170 species, of which some 10 per cent. are endemic. The remainder are all found in the continental part of the region.

Region of the South Temperate Oceanic Islands

Scattered far from land in the ocean which surrounds the Antarctic continent are a number of islands, very small in size and with but a slight vegetation, but, on

account of the distribution and affinities of their tiny floras, forming one of the most interesting of phytogeographical regions.

These islands are, with their situations :

1. South Georgia.	54° S. : 36° W.
2. The Tristan da Cunha group	37° S. : 10° W.
3. Marion Island	46° S. : 38° E.
4. The Crozets	46° S. : 50° E.
5. The Kerguelen group	48° S. : 70° E.
6. Heard Island	52° S. : 72° E.
7. Amsterdam and St. Paul Island	37° S. : 78° E.
8. Macquarie Island	55° S. : 160° E.

Floristically belonging to this group are the Antarctic continent and the South Shetland Islands, but the former has only two species of flowering plants, both South American, and the latter one, also South American, and they need not be considered further.

Considering the varied latitude of the islands their flora is remarkably constant and there is strong relationship between the islands. A compilation made by the writer from various sources shows that the number of species which may safely be regarded as native is 84, of which no fewer than 34 belong to the Cyperaceae and Gramineae. These latter, it is interesting to note, are appreciably less widely distributed over the islands than the rest, and their endemism is higher, namely 20/34 as compared with 17/50.

In the following analysis it saves a great deal of space and repetition if the various constituent parts of the region are referred to by the numbers attached to them above.

The floras of the constituent parts are :

1	has 10 species, of which 1 is endemic.
2	„ 33 „ „ 19 are endemic.
3	„ 8 „ „ none is endemic.
4	„ 6 „ „ none is endemic.
5	„ 21 „ „ 4 are endemic.
6	„ 5 „ „ none is endemic.
7	„ 17 „ „ 7 are endemic.
8	„ 29 „ „ 1 only (?) is endemic.

Of the 84 species in total 37 species are endemic to the region as a whole, and 62 occur on one island or island group only, *i.e.* 3 on 1, 27 on 2, none on 3, none on 4, 6 on 5, none on 6, 9 on 7, and 17 on 8, this last number being no doubt influenced by the proximity of New Zealand.

Ten species occur on two islands or groups out of the eight in the combinations 15, 27, 27, 27, 27, 56, 57, 58, 58, 78, the endemics being underlined.

Five species occur on three islands or groups out of the eight in the combinations 145, 158, 278, 356, 458.

Three species occur on four islands or groups out of the eight in the combinations 1358, 3456, 3458, namely *Montia fontana*, *Pringlea antiscorbutica* and *Crassula moschata*.

Four species occur on five islands or groups out of the eight in the combinations 12378, 13458, 13568, 34568, namely *Ranunculus biternatus*, *Acaena adscendens*, *Callitriche antarctica* and *Azorella Selago*.

Of the species which are not endemic to the region, the affinity lies, as might be expected, chiefly with Australasia and temperate South America. Thus there are :

Outside the region in Australasia only	16
" " " " South America only	12
" " " " both the above	6
Remainder	13

The six which range from America through the islands to Australasia are :

Acaena adscendens, *Agrostis magellanica*, *Azorella Selago*, *Callitriche antarctica*, *Crassula moschata* and *Juncus scheuchzerioides*.

The wider species include six variously distributed in the southern hemisphere ; three found in the northern temperate zone and in South America ; and four more or less cosmopolitan. The distribution of these within the region is respectively :

2, 27, 2, 7, 27, 2 : 1, 2, 5 : 7, 8, 1358, 28.

It will thus be seen that only one species widely distributed outside the region is also widely distributed in it, and further that the six wide southern species, as they may be called, are found only on the Tristan group and/or on Amsterdam and St. Paul, that is to say, on the two equally most northern island groups.

CHAPTER 11

THE DISTRIBUTION OF SPECIES—IV

THIS chapter, which concludes the general survey of the geographical distribution of species, is devoted to certain particular aspects of the subject, namely: discontinuous species; species with very narrow ranges; species pairs; and, finally, the three types of Angiosperms which are particularly associated with marine and maritime habitats and which therefore differ fundamentally in geography from all the rest.

Discontinuous Species

Just as in families and genera, a proportion of all species have ranges consisting of two or more constituent and separate parts, and some have actually been mentioned in Chapter 8. There are, however, two reasons why it is impossible here to give more than a very brief account of these. In the first place they are very numerous and any attempt to deal with them critically and systematically would be far beyond the scope of this book; and, in the second place, the detailed account that has already been given of discontinuous genera applies in outline almost equally well to species. Indeed, genera often owe their discontinuity to that of one or more of their constituent species.

For these reasons no more is aimed at here than to demonstrate the great variation in the range of discontinuous species and the fact that they can be classified in the same way as discontinuous genera. It must also be pointed out that the different examples cited, though taken from reliable sources and authorities, have not been critically examined and verified in the same way as was done for the genera, and some of the details may well prove, on closer examination, to need qualification or correction.

It will be remembered that there are, in correlation with the major circumstances of world geography, four principal types of generic discontinuity, and species also are conveniently dealt with under these heads. The fifth, Hawaiian, category can here be ignored.

Discontinuous species of the northern extratropical zone

A number of species are found discontinuously distributed throughout the northern temperate zone. *Potentilla fruticosa*, for example, is found in North America, in Europe, in Siberia and in the Himalayas, and amongst others with a rather similar type of range are *Anemone multifida*, *Arabis alpina* and *Ostrya carpinifolia*.

Probably more numerous are what may be termed transatlantic species, which occur in parts or all of North America and in the western part of the Eurasian continent. As might be expected, some at least of these occur in the British Isles, and among them are *Eriocaulon septangulare*, *Spiranthes Romanzoffiana* and *Lobelia Dortmanna*. *Solidago sempervirens* is said to occur in North America and on the Azores.

The remarkable eastern North American-eastern Asiatic type of range so well known among genera is seen in a number of species, among them being *Acer rubrum*, *Cypripedium arietinum*, *Polygonum arifolium*, *P. scandens*, *P. virginicum* and *Symplocarpus foetidus*.

In the New World several species are found on the west and east sides of the continent, but not in between, including *Danthonia intermedia*, *Oxytropis foliosa* and *Senecio resedifolius*.

Similarly in the Old World there are species such as *Betula humilis*, which occurs in Europe, Central Asia and eastern Asia.

Many examples of discontinuity on a smaller scale are afforded by the floras of Europe and the Mediterranean. The familiar *Rhododendron ponticum* grows on the south coast of the Black Sea, in parts of Palestine, and in the extreme south part of the Iberian Peninsula. *Potentilla apennina*, *Genista dalmatica*, *Althaea rosea*, *Phlomis lanata* and several others are found in Italy and Bulgaria only, while *Crocus veneris* and *Centaurea cretica* occur on the islands of Cyprus and Crete. *Androsace villosa* has recently been recorded from the Atlas Mountains, having long been familiar in the Alps and the Balkans. On a still narrower scale *Pedicularis rosea* and *Saxifraga retusa* are discontinuously distributed within the Alpine mountain system.

Lastly, there may be mentioned here several north temperate plants which have been recorded, apparently wild, in one or more spots in the tropics, usually on mountains. *Drosera longifolia* is said to occur on one mountain in the Hawaiian Islands; the European *Luronium* (*Elisma*) *natans* was collected in Java in 1932; *Scirpus setaceus* is known also from New Guinea; and *Sparganium simplex* has been found in Sumatra.

Discontinuous species of the tropical zone

There are certainly a number of species which are found wild both in tropical America and in tropical Africa, though it would be rash to say that all the following, which have been so described, are undoubtedly native in both continents:

Alternanthera repens, *Andira inermis*, *Clitoria Ternatea*, *Dalbergia Ecastapii*, *Ilum*, *Drepanocarpus lunatus*, *Echinochloa crus-pavonis*, *Eulophia alta*, *Fleurya aestuans*, *Gossypium hirsutum*, *Hyparrhenia rufa*, *Hypogynium spathiflorum*, *Mucuna urens*, *Neurotheca loeselioides*, *Oplismenus hirtellus*, *Peperomia pellucida*, *Sauvagesia erecta*, *Sida linifolia*, *Tragia volubilis* and *Wissadula amplissima*.

Hibiscus diversifolius and *Jussiaea erecta* are said to occur on Madagascar or the Mascarenes as well as on the two continents.

Closely related to the above are *Ludwigia palustris*, which is found throughout America, Europe and Africa; *Hydrocotyle umbellata* in America, South Africa, Madagascar and the Mascarenes; and *Hydrocotyle verticillata* in America, South Africa and Hawaii.

A few species, among them *Arundinella hispida* and *Caesalpinia major*, occur in America and in Asia and the Pacific Islands, and in connection with these the reader may be reminded of one of the most remarkable of all discontinuous species, *Nertera depressa*, which is found in Central and South America, Hawaii, Tristan, Australia and New Zealand, south-east Asia and Malaya.

Many species link Africa and Asia (and often the Pacific Islands), as, for instance, *Abutilon pannosum*, *Albizzia Lebbeck*, *Canscora decussata*, *Grangea maderaspatana*, *Hibiscus micranthus*, *Hyptis suaveolens*, *Mundulea sericea*, *Ormocarpum*

senoides and *Phyllanthus reticulatus*. Rather special cases are *Hypericum mysorense* in Socotra and India; *Trapa natans* in Europe, Africa and Asia; and *Sambucus adnata* on the East African mountains and in the Himalayan region.

Alectra arvensis, *Pipturus velutinus*, *Procris pedunculata*, *Tournefortia sarmentosa* and *Trichodesma indicum* occur in Asia and in Madagascar or the Mascarenes (but not on the continent of Africa), and *Carex brunnea* is similar but extends also to Australia and Hawaii.

Among species on Madagascar as well as on the two continents may be mentioned *Dumasia villosa*, *Eragrostis aspera*, *Hibiscus lobatus*, *Hyptis lobata*, *Neyraudia madagascariensis* and *Sacciolepis curvata*.

Andropogon Gayanus, *Elyonurus Royleanus* and *Panicum maximum* are said to link the Cape Verdes with the African continent. *Erica arborea*, which is found in Madeira, the Canaries, the Mediterranean and on the East African and Cameroon Mountains, provides a similar link further north.

Tropical discontinuity of a less wide kind is best seen in Asia and the Pacific Islands, where there are many remarkable examples. It is particularly common between continental Asia and the Malayan Archipelago, and is exemplified on the one hand by *Alchemilla javanica*, *Anaphalis contorta*, *Avena Junghuhnii*, *Festuca leptopogon*, *Hydrangea oblongifolia*, *Neillia thyrsiflora*, *Photinia Notoniana*, *Potentilla Mooniana*, *Rhopalocnemis phalloides*, *Rubus lineatus*, *Schisandra elongata* and *Valeriana Hardwickii*, which are known from India and the Himalayas and from the Archipelago, and, on the other, by *Anotis Wightiana*, *Damnacanthus indicus*, *Potentilla sundaica*, *Rubus niveus* and *Rubus pectinatus*, which link the Archipelago with China and Japan. *Eriocaulon Hookeri* is recorded from the Malay Peninsula and from Borneo, and *Melochia arborea* from Indo-Malaya and Christmas Island.

Within the Archipelago *Albizzia scandens*, *Dalbergia subalternifolia*, *Dinorchloa ciliata*, *Erythrophleum densiflorum*, *Gardenia Merrilli* and *Omphalea malayana* are all found on Borneo and the Philippines, and there are doubtless other species linking other islands.

Discontinuity involving Australasia and the Pacific Islands is naturally very varied, and it must suffice to illustrate it by the following instances:

<i>Carex Graeffeana</i>	.	.	Philippines, Java, Fiji.
<i>Alstonia plumosa</i>	.	.	New Caledonia, Fiji, Samoa.
<i>Cyathodes Tameiameiae</i>	.	.	Hawaii, Tahiti.
<i>Casuarina Cunninghamii</i>	.	.	Australia, New Caledonia.
<i>Solanum aviculare</i>	.	.	Australia, New Zealand, New Guinea, Philippines.
<i>Didiscus procumbens</i>	.	.	Australia, New Guinea, New Caledonia.
<i>Geranium ardjunense</i>	.	.	Australia, New Zealand, Malayan Archipelago.
<i>Microlaena stipoides</i>	.	.	Australia, New Zealand, Philippines, Hawaii, Java.
<i>Gahnia Gaudichaudii</i>	.	.	New Zealand, Hawaii.
<i>Carex uncinata</i>	.	.	New Zealand, Chatham Islands, Hawaii.

Discontinuity in the southern extratropical regions

Because it has such a direct bearing on the history of the land masses of the southern hemisphere, this type of discontinuity is perhaps the most interesting and important of all, and several incidental references have already been made to it.

One of the commonest subsidiary types of range is that between New Zealand and South America such as is shown by *Enargea marginata* and *Agrostis magellanica*. *Edwardsia microphylla* is similar but occurs also in Juan Fernandez, on Easter Island and on Gough Island. *Aristotelia peduncularis*, *Epilobium junceum*, *Lilaeopsis lineata*, and probably *Tetragonia expansa*, exemplify discontinuity between both Australia and New Zealand on the one hand, and South America on the other. *Oxalis magellanica* is very like these but is recorded from New Guinea and in the New World ranges north to Bolivia. *Coriaria ruscifolia* is a very noteworthy species which is found not only in South America and New Zealand but also in the Kermadecs, Fiji, Samoa and Tahiti.

Lobelia anceps is found in all three southern continents, *Papaver horridum* connects South Africa with Australia, and *Pelargonium acugnaticum* links South Africa with New Zealand. *Chevreulia stolonifera* is found on Tristan da Cunha and in South America, and *Phylla nitida* on Tristan and in South Africa.

In the Australasian region discontinuity on a smaller scale is not uncommon, and there are, for example, many species found in both Australia and New Zealand. *Disphyma australis* occurs in Australia, in New Zealand and on the Chatham Islands, *Gaultheria depressa* in Tasmania and New Zealand, and *Acaena anserinifolia* in New Zealand, Tasmania and New Guinea. *Melicytus ramiflorus* ranges from New Zealand to Norfolk Island, the Kermadecs, Tonga and Fiji.

The problems of these geographical relationships in the southern hemisphere have been studied by many botanists, notably by Du Rietz (274), Skottsberg (224, 225, 228, 230) and Oliver (177).

Discontinuity between the northern and southern extratropical regions

This type of species distribution must be approached with great caution, because of the difficulty of saying with any degree of certainty that the occurrence of a northern plant in the south, and particularly in Australasia, is natural and not the result of accidental introduction in the course of human settlement. Quite frequently, for instance, such species have been recorded from Australia or New Zealand but nearly always some suspicion attaches to their presence in these countries. Since to consider these cases critically is impossible here, it is best to say as little as possible about them and to mention simply a few plants which appear to occur naturally somewhere or other in both hemispheres.

Primula farinosa is one of the best examples, being fairly widely distributed in the northern temperate zone and occurring also in temperate South America. *Elatine americana* is recorded from North America, from Australia and from New Zealand, while *Epilobium tetragonum* is found in Europe, and in the same two southern countries. *Ranunculus parviflorus* is said to occur in the southern United States, in the West Indies, in Europe, the Mediterranean region and the Canaries, as well as in Australia and New Zealand. Other species generally regarded as discontinuous between some part of the northern temperate and some part of Australasia include *Barbarea vulgaris*, *Geranium dissectum*, *Geum rivale* and *Geum urbanum*. Other rather different examples are *Lepturus cylindricus* in the Mediterranean and in South Africa, two or three species of *Anemone* discontinuous between the southern United States and temperate South America; and *Wahlenbergia gracilis*, found in India, New Caledonia, Australia and New Zealand.

Species Pairs

In comparing the floras of two regions it is generally easy to see that certain species in one are perfectly distinct from any species in the other. Similarly, unless the floras are very different from one another there will generally be found some species that are common to both. In addition, however, to these well-marked differences and resemblances it will often be found that there are in the one flora certain species so closely similar to species in the other that it is difficult to say whether they should be regarded as identical or not. If the difference between them is very slight indeed, they will tend to be recognised as belonging to one and the same species, but if larger differences can be demonstrated, they will tend to be separated into two closely related species. In these latter circumstances the two closely similar species are generally referred to as vicarious species or as a species pair. In each pair one species is the geographical counterpart or representative of the other.

Since it may be assumed that the species of a pair have generally descended from a comparatively recent common ancestor, the prevalence of such pairs helps to indicate the degree of relationship between floras. Many such species pairs can, for instance, be noted in the floras of North America and Eurasia, or even in different parts of one or other of these regions. The American *Cornus canadensis* is the New World counterpart of the Old World *C. suecica*; the American *Maianthemum canadense* represents there the Eurasian *M. bifolium*; *Epigaea repens* parallels *E. asiatica*; and there are several others.

It is not, however, altogether easy to give an account of such pairs, because the recognition of them depends so much on individual taxonomic conceptions. One authority may regard certain plants of one region as identical with those of another, while another may reckon them to form two distinct but vicarious species. This again is often the case as regards North America and Eurasia, where, for example, the American form of *Hepatica* is sometimes regarded as distinct from the European *Hepatica triloba* and therefore to form with it a species pair. Much the same is true of *Anemone nemorosa* and *A. quinquefolia*, *Oxalis Acetosella* and *O. montana*, *Luzula pilosa* and *L. saltuensis*, *Vallisneria spiralis* and *V. americana*, *Ranunculus Flammula* and *R. laxicaulis*, and *Scrophularia nodosa* and *S. marilandica*. The western European *Littorella uniflora* is sometimes regarded as distinct from the North American plant, and differences have recently been demonstrated between the representatives of the genus *Lysichitum* on either side of the Bering Strait.

But whether these distinctions are justifiable or not is really beside the point. Their important aspect is that they demonstrate very vividly the fact that the difference between the species of any two floras need not be great but may in fact be of almost any value.

The examples just mentioned are particularly problematical ones and species pairs are generally much more clear cut. They occur, moreover, in almost every part of the world. North America once more has several pairs between the eastern and western coasts as, for instance, *Carex misandroides* and *C. petricosa* and *Arenaria marcescens* and *A. obtusiloba*.

Turrill (247) lists a number of pairs between Spain and the Balkans. *Prunus lusitanica* in Spain is the counterpart or pair of *Prunus Laurocerasus* in the Balkans; and others are *Hypericum Coris* and *H. empetrifolium* and *Nonea alba* and *N. ventricosa*.

One of the most familiar pairs is afforded by the two "alpenrosen" of the Alps, *Rhododendron ferrugineum* and *R. hirsutum*. These are of special interest because their ranges are to some extent coterminous, but one is found on granite rocks and the other on calcareous rocks.

Skottsberg (227) mentions several pairs between Java and Hawaii, including *Gahnia javanica* and *G. Gaudichaudii* and *Vaccinium variegatifolium* and *V. peleanum*. Similarly between Juan Fernandez and Hawaii there are pairs in *Cladium scorpoideum* and *C. angustifolium* and in *Plantago fernandezia* and *P. principis*. *Distylium stellare* in the Malayan Archipelago is the counterpart of *D. indicum* in Khasia.

In the southern hemisphere too there are interesting pairs. The New Zealand species *Drosera stenopetala*, *Oxalis lactea*, *Donatia novae-zelandiae*, *Pratia angulata* and *Gaimardia setacea* are represented in South America by *Drosera uniflora*, *O. magellanica*, *Donatia fascicularis*, *P. repens* and *G. australis* respectively. Even between New Zealand and Norfolk Island at least two pairs have been noted.

Narrowly Restricted Species

It is inherent in the cycle of distribution described in Chapter 3 that an increase in the range of a species (or other unit) is usually associated with or accompanied by an increase in the number of individual plants comprising the unit and that the reverse is also true. A species is envisaged as increasing the number of its individuals up to a maximum and thereafter diminishing until none is left and extinction results. From this it follows that species which are either very young or very old will, for quite different reasons, consist of a comparatively limited number of individuals and that their ranges will be correspondingly small. This view has already been elaborated under the heading of endemism, but something more must be said about it here.

On this argument it is clear that species may in fact consist of any number of individuals, but it is equally obvious that there is a definite lower limit to the number because no species exists unless there is at least one individual of it. Thus the minimum range of a species is the area occupied by a single individual plant. The actual spatial value of this range will, of course, depend on the size and character of this individual.

It is naturally almost impossible to maintain that any particular species does in fact consist of only one individual, but there are several cases in which only one individual has ever been seen or recorded. Probably the most authentic is that of *Franklinia Alatomaha* (80) which has already been mentioned on p. 119, but there are other rather similar examples such as *Shortia galacifolia*.

Melliss (168) in his account of the island of St. Helena cites *Pharnaceum acidum*, which he says in his day survived only as a single plant and which since then has perhaps disappeared entirely.

Since the one-individual condition is likely to persist longer if it has resulted from the gradual dying out of a species than if it is the result of the recent origin of a species, there is a strong presumption that actual cases of one-plant species represent species on the verge of extinction, and it is interesting to note in this connection that there appear to be no instances in which a species has been found first as a single individual, and later as many individuals obviously descended from this parent. More often the original discovery has never been repeated.

Ridley (202) has collected some interesting data on this point. He found *Didymocarpus Perditus* in the vicinity of Singapore on one occasion, but it has never been seen again either there or elsewhere. The same is true of *Strophanthus Maingayi*. *Melastoma molle* has been found once in Singapore and once in the Philippines, while *Endopogon Ridleyi*, *Zingiber chrysanthum*, *Pinanga singaporensis* and *Euthemis minor* have all disappeared owing to the destruction or modification of their only known habitats.

Willis (262) quotes the case of *Coleus elongatus*, which he says consists of a dozen or so plants on the mountain of Ritigala in Ceylon. This species is closely related to *Coleus barbatus* which has a much wider range but which is also found on this mountain, and there is an inference that it has been derived from it, so that this may be a case of a new species, and it may be noted that it is known from appreciably more than a single plant. But these are all exceptional cases and normally even markedly restricted species have more individuals.

Although there is no necessary difference between them it is convenient in surveying restricted species in general to distinguish between those which occur on very small islands and those which occur very locally in parts of larger continuous land areas. The former tend to be more conspicuous when recorded in print, because their bounds are so definitely and unmistakably laid down, whereas in the latter it is generally very difficult to convey in words the actual area which they cover. It is perhaps for this reason that an impression is gained that very narrow species are particularly associated with small islands, but whether this is really true could hardly be decided without a very long and tedious investigation. There are *prima facie* reasons why it may be so, notably because, unless it can escape to other islands, the maximum range attainable by a species originating on an island is the area of that island itself. On the other hand, most of the islands bearing very narrow species are not themselves very isolated but are often members of archipelagos, where the problem of dispersal between islands can scarcely be regarded as insuperable. There is also the question whether species production with its inevitable endemism may not be favoured by narrowly insular conditions which are, of course, only one form of geographical isolation, but this is a question which it is difficult to answer. It does seem, however, that certain families and genera are specially characterised by these very narrow insular species.

The case of the palms, in particular, has already been mentioned, and is worth reconsideration in the light of what has just been said, but almost any systematic monograph reveals something of the sort.

The genus *Weinmannia*, for instance, has among its species *W. camaguiensis* from Camagui Island in the Philippines, *W. comoroensis* on Johanna Island in the Comoros, *W. vitiensis* and *W. spiraeoides*, each from one island in the Fiji group, *W. fraxinea* from Honimo Island in the Moluccas, *W. Denhami* and *W. Macgilivrayi* from a single island in the New Hebrides. Several comparable instances in *Begonia* have already been mentioned in Chapter 8.

Practically all the more isolated small islands other than mere coral atolls afford examples, as, for instance, Christmas Island with at least three endemics, and Easter Island with four, but there are many on islands which are far from isolated, including *Cakile alacranensis* from the four islands of the Alacran Reef off Yucatan (173).

In the Bahamas Taylor (242) has emphasised the same thing, especially in the island of Inagua, which has no fewer than thirteen endemic species. Taking the

archipelago as a whole also there are seven endemic species of *Agave*, four of them on one island only.

Coprosma is another genus with some very narrow insular endemics. Oliver (178) includes two from the Kermadecs, one from Chatham Island, two from Raiatau, and one each from Rarotonga, Pitcairn, Masa Tierra and the Tuamotus.

Still other examples are *Maerua Dupontii* from Aldabra Island, *Rapinia collina* from a tiny island off New Caledonia, *Aulacocarpus crassifolius* from Gorgona Island, *Rhipsalis megalantha* from San Sebastian Island near Rio de Janeiro, *Sesuvium distylum* from Fernando Noronha, and a species of *Xeronema* from two very small islands off New Zealand.

There are also many instances of very narrow ranges on larger land surfaces, among them being certain New Zealand species (179). The work of Fernald and Marie Victorin on the floras of the shores of the Gulf of St. Lawrence (see Chapter 10) also includes references to a number of such plants, among them being *Cirsium mingaanense*, from a few spots on the Mingaan Islands; *Solidago Victorinii* and *S. anticostensis*, very locally distributed on Anticosti; and several species of *Crataegus* and *Gentiana* from other parts of the Gulf. Elsewhere, too, Fernald (80) has listed a number of plants of specially narrow range in North America, perhaps the most striking example being *Neviusia alabamensis*, of which only a single colony is known.

Similar examples can in fact be found in almost every part of the world, and especially from mountain regions, where the different peaks tend to produce much the same isolation as is afforded by small islands (see above), and, in short, narrowly restricted species are to be found as a small but normal constituent of nearly all floras.

The Distribution of the Marine Angiosperms, or "Sea Grasses"

(Plate 15)

There is one small group of flowering plants so different from all the rest in character and habitat that their geography merits very special attention in any general survey of plant distribution. This group consists of a small number of genera which live actually completely submerged in the shallow coastal waters of seas and which are popularly called the "sea grasses."

The distribution of these plants has been described in detail by Ostenfeld in a number of papers, and the data have been collected together and illustrated by a series of maps (111).

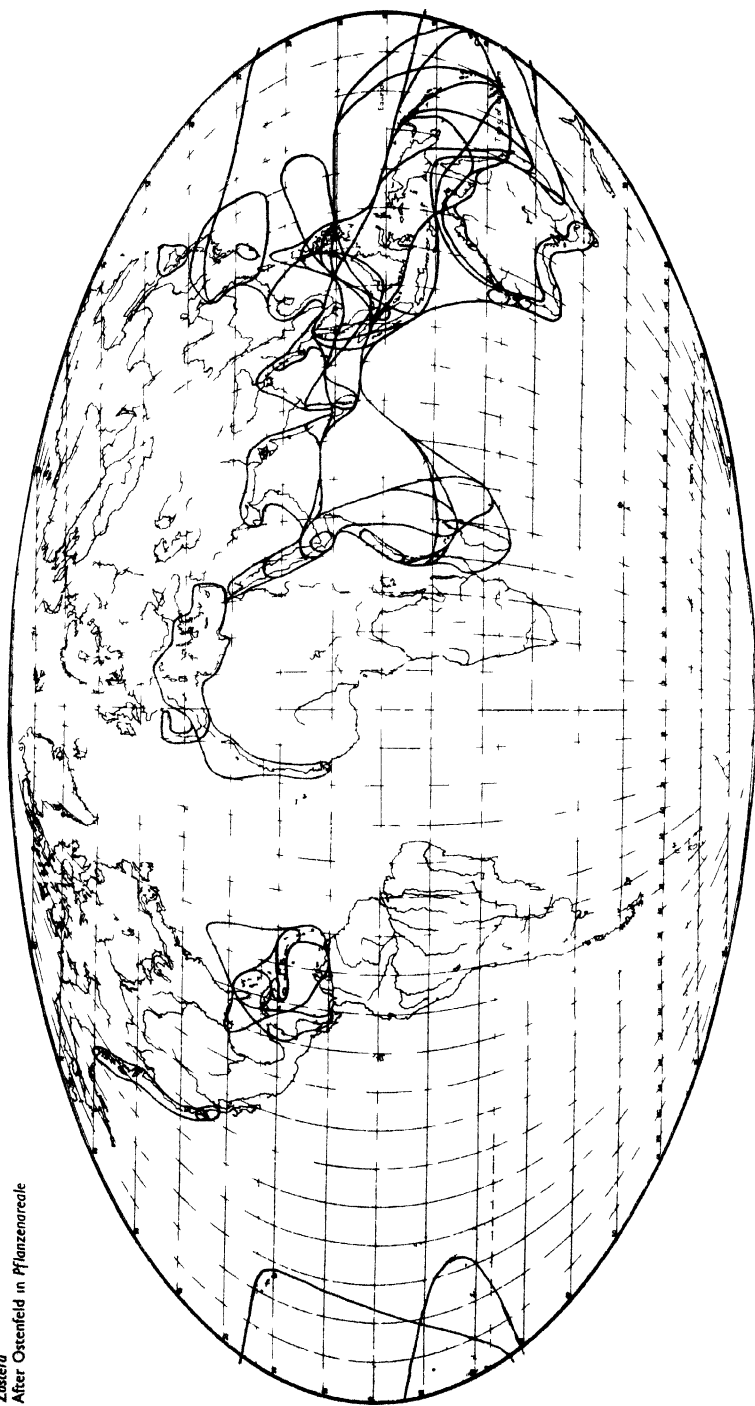
There are eight genera concerned, three of them, *Zostera*, *Phyllospadix* (fig. 50) and *Posidonia*, being found in temperate waters, and the rest in tropical seas.

The genus *Zostera* has been divided into eleven species distributed as follows:

<i>Zostera marina</i>	.	.	.	northern temperate seas.
<i>Z. caespitosa</i>	.	.	.	Japan.
<i>Z. asiatica</i>	.	.	.	Japan and Korea.
<i>Z. caulescens</i>	.	.	.	Japan and Korea.
<i>Z. japonica</i>	.	.	.	Japan and Sakhalin.
<i>Z. nana</i>	.	.	.	North Atlantic Europe.
<i>Z. capensis</i>	.	.	.	South Africa.
<i>Z. capricorni</i>	.	.	.	Australia.
<i>Z. Muelleri</i>	.	.	.	Australia.
<i>Z. novaezelandica</i>	.	.	.	New Zealand.
<i>Z. tasmanica</i>	.	.	.	South Australia and (?) Tasmania.

Map of the World showing the distribution of the
species of Marine Angiosperms excluding the genus
Zostera
After Ostenfeld in *Pflanzenreich*

PLATE 15



Area correct. This is increasing towards border of map.
Approximate Scale 1,000,000 (1600 miles) along Equator
on Mollweide Homographic Projection

Copy 4



FIG. 50.—*Phyllospadix Scouleri*, about natural size, after Engler.

Posidonia with two species shows great discontinuity, one species being Mediterranean and the other South Australian.

Phyllospadix has three species. Two of these overlap on the west coast of North America from California northwards, and one of them reaches to Alaska. The third species is on the Liu Kiu Islands on the opposite side of the Pacific.

The five tropical genera (fig. 51) comprise 23 species. It is unnecessary to describe their ranges in detail as these can be seen on the map, and it will be enough here to tabulate the leading points relating thereto which are not altogether apparent there. They are:

1. Only one species, *Thalassia testudinum*,¹ is in both the Old and New Worlds. It occurs in eastern America and in the Indian Ocean, so that even here there is complete oceanic segregation.

¹ This is now often considered to consist of two species, one in each hemisphere, in which case there is no species common to both Old and New Worlds.

2. Seventeen out of the other 22 are found only in the Old World, a preponderance scarcely surprising in view of the immensely longer coast-lines there.

3. The other 5 species are all confined to America. All are east coast species and confined to the shores of the Caribbean, so that they have rather restricted ranges.



FIG. 51.—*Cymodocea ciliata*, a tropical marine Angiosperm, about natural size, after Engler.

4. There is only a single species on the west coast of Africa, and this is a Mediterranean one which reaches down the coast to Senegambia.

5. Another species is confined to a very restricted part of Western Australia.

6. All the rest, 15 in number, inhabit the Indian and Pacific Oceans and divide into those which occur in East Africa and those which do not.

7. Of the 10 species which do so, 8 are found in some part of Madagascar, etc.

8. Of the 5 non-African species, 3 reach from some part of Asia to Australasia or the Pacific Islands ; one is found from Ceylon to Borneo ; the other in the Liu Kiu Islands.

9. Of the 10 found in East Africa, 5 reach Asia, Australasia and the Pacific Islands ; 3 reach Asia and Australia ; one is discontinuous between Africa and Australia, and the last is confined to Africa and Madagascar, etc.

Such are the more general features of the distribution of these plants, and much the most striking of them are the segregation in the hemispheres and the absence from the west coasts of the American and African continents. There are also the following minor features, which are partly shown on the map but which are more apparent in the original publication :

1. Of the 11 species which reach the Red Sea, 6 cover practically all of it ; 3 cover only the southern half ; and 2 only touch south-west Arabia or Aden.

2. Of 8 species in Madagascar, etc., 5 occur only in the north of Madagascar ; 2 in the north of Madagascar and on Mauritius ; and one covers the Comoros and all Madagascar.

3. Of 6 species in India, 3 are only in Ceylon ; 2 are only in Ceylon and south India ; and one only is all round the coasts.

4. Of 13 species in Australia, 7 are confined to the north or north-east ; 5 are local elsewhere, and only one is on all coasts.

5. Of 7 species in the Pacific Islands, 6 are restricted to the western groups ; only one reaches further east, and there is none in Hawaii.

These latter points clearly reveal that, despite the differences in specific distributions, there are nevertheless certain prevalent range limits. The possible significance of these will be discussed later (p. 280).

Mangroves

(Plate 16)

Mangrove forests are found in muddy tidal waters along much of the coasts of the tropics and occasionally outside. The flora is a very specialised one, consisting of the mangroves proper, shrubs and small trees belonging to about half a dozen genera, and a few associated species rarely or never found elsewhere. The number of species of mangroves and the more commonly associated species may be reckoned at about thirty.

In many respects the distribution of the species is reminiscent of that of the marine Angiosperms, but, as the following list will show, there are a number of other interesting points about them :

1. No species is at all completely distributed over the coasts of both hemispheres.

2. There is complete segregation between the species west of Africa and those to the east.

3. There are only 4 species in the New World, i.e. *Rhizophora Mangle* and *R. racemosa* on the east coast, and *Laguncularia racemosa* and *Avicennia nitida* on both coasts. *R. racemosa* and *L. racemosa* occur also in West Africa, while *R. Mangle* has been found in the Pacific Islands.

4. Species of the East African coasts number about 8 : 5 extend east to the Pacific Islands ; 2 to Malaya (*Ceriops Candolleana* and *Avicennia officinalis*) ; and the other, *Avicennia marina*, reaches Madagascar, etc. only.

5. Of the rest no fewer than 7 range from India to some part of the Malayan Archipelago, and 3 from India to Australasia or the Pacific Islands. *Avicennia alba* and *A. sphaerocarpa* range from continental south-east Asia into Malaya; *Sonneratia apetala* and *Avicennia lanata* are in continental south-east Asia only.

6. *Avicennia eucalyptifolia* ranges from Malaya to Australia; *A. Balanophora* is in Australia only; *A. resinifera* is in Australia and the Pacific Islands; and *A. tomentosa* is in the Malayan Archipelago.

7. No species occur in Hawaii.

8. The concentration of species in tropical Asia is more marked than in the marine Angiosperms, as the following tabulation into areas shows:

western America	eastern America	West Africa	East Africa	Madag.	India	S.E. Asia	Malaya	Aus- tralia	Pacific Islands
2	4	3	8	9	18	23	23	10	12

The distribution of the mangroves thus follows in quite a number of ways that of the marine Angiosperms, and other points of resemblance could be made did space permit. For instance, here again we find that nearly all the species in India are on the south coast or in Ceylon. Perhaps the main difference from the marine Angiosperms is the occurrence of species on both sides of the Atlantic and on both coasts of America.

The Distribution of Strand Plants

A considerable number of flowering plants are found only on sandy sea beaches or in the vegetation immediately behind these beaches. Some of these, like *Cakile maritima* and *Salsola Kali*, occur in temperate latitudes, but the most characteristic are restricted to the warmer parts of the world and there form an assemblage of plants which are conveniently referred to as "strand plants."

It is not always easy to say exactly what species should be included here, and for this and other reasons no complete statistical account of them can be given, and it must suffice to refer to the distribution of some of the more noteworthy. This is enough to emphasise the main feature of their geography, which is that they are more generalised in range than either the marine Angiosperms or the mangroves.

Some of them occur, apparently naturally, on almost all tropical coasts wherever the substratum is suitable for their development, among these being *Cassipoua filiformis*, *Dodonaea viscosa*, *Hibiscus tiliaceus*, *Ipomoea Pes-caprae* and *Thespesia populnea*. These species show little segregation between continents or between the opposite sides of continents, a point which is also shown on a smaller scale by *Dalbergia Ecastaphyllum* and *Drepanocarpus lunatus*, which occur on both sides of the Atlantic, and by *Batis maritima* and *Hippomane Mancinella*, which are found on both coasts of tropical America.

At the same time many of the best-known and most widespread of these plants do not extend further west than East Africa, and it is the Indian and west Pacific Oceans that are especially the home of strand plants. These Old World wide species include *Casuarina equisetifolia*, *Cordia subcordata*, *Calophyllum Inophyllum*, *Barringtonia racemosa*, *Pongamia glabra*, *Pemphis acidula*, *Guettarda speciosa*, *Scaevola Koenigii* and *Tournefortia argentea*.

Characteristically Asiatic species, often extending into Australasia and the

Pacific Islands, include *Crinum asiaticum*, *Dolichandrone Rheedii*, *Samadera indica* and *Triumfetta subpalmata*.

On the other hand there are a few distinctively New World species, most of which occur only on the east coast of America, and among these are *Coccolobis Uvifera*, *Euphorbia buxifolia* and *Omphalea triandra*.

There is a general tendency for Old World species to be present somewhere in the Pacific, a fact that is no doubt correlated with the enormous number of small islands there, and this region has therefore probably a larger population of strand plants than any other, although south-east Asia and the Malayan Archipelago run it close. It is also noteworthy that among these beach plants several, in contrast to the marine Angiosperms and mangroves, reach Hawaii.

CHAPTER 12

THE HISTORY AND DISTRIBUTION OF THE BRITISH FLORA

THE fossil history of the Angiosperms, which is described at some length in Chapter 14, shows clearly enough that the floras of to-day can be understood properly only if the past is also taken into account, and so, in discussing the distribution of the plants living in the British Isles to-day, due notice must be taken of their history. Much of this history is, however, so remote in time that it does not directly concern the actual species which now compose the flora, and it will be sufficient here to trace the story of these plants particularly from the time at which they became inhabitants of Britain. Fortunately this story of the British flora, that is to say of the assemblage of species which now forms the vegetation of the British Isles, starts at a definite point in geological time, beyond which it is not necessary to probe.

As will be seen in Chapter 14, the vegetation of the northern temperate latitudes remained more or less constant, presumably under the influence of equally constant climatic conditions, throughout the Cretaceous and most of the Tertiary epochs, but in the Pliocene period there began a rapid deterioration of climate, accompanied by marked floristic changes, and this deterioration culminated in the Ice Ages of the Pleistocene period.

It so happens that one of the last stages before the oncoming of the ice, namely the Upper (later) Pliocene, has, in the British Isles, left behind it remains so clear that they give a good picture of the contemporary plant life. These remains are the fossils of the Cromer Forest bed and their outstanding feature is that they are almost the same species that are living in Norfolk to-day.

It is possible to say, therefore, with some confidence that at the close of the Pliocene the flora of Britain was very much as it is to-day and that its subsequent history is that of the vicissitudes through which it has passed since that time.

The Cromer Forest bed contains remains not only of plants but also of animals, and these latter are in many ways the more striking. For instance, there have been described from among them no fewer than forty-six species of mammals, including such types as elephant, hippopotamus, rhinoceros, musk ox, glutton and a number of deer. Thirty of these were large animals and of these only six are known anywhere to-day, the remainder having become extinct, while of these six only three now inhabit the British Isles. It is, however, only in the mammals that there is any conspicuous difference between the past and present; the other vertebrates in the deposit are all species now living in the country, and the same is virtually true of the molluscs. Similarly with the plants, of which sixty-eight species have been identified, only some half-dozen, including *Trapa natans*, *Ranunculus nemorosus*, *Hypochaeris procumbens* and *Najas minor*, are no longer to be found here. All the rest are species still familiar to British botanists, and these give ample evidence that the flora as a whole must have been very similar to that existing to-day (196).

What has been said about the mammals does not invalidate the comparison, because their disappearance can be explained by the differences in the distribution of land and sea as between the past and present. There are good reasons for

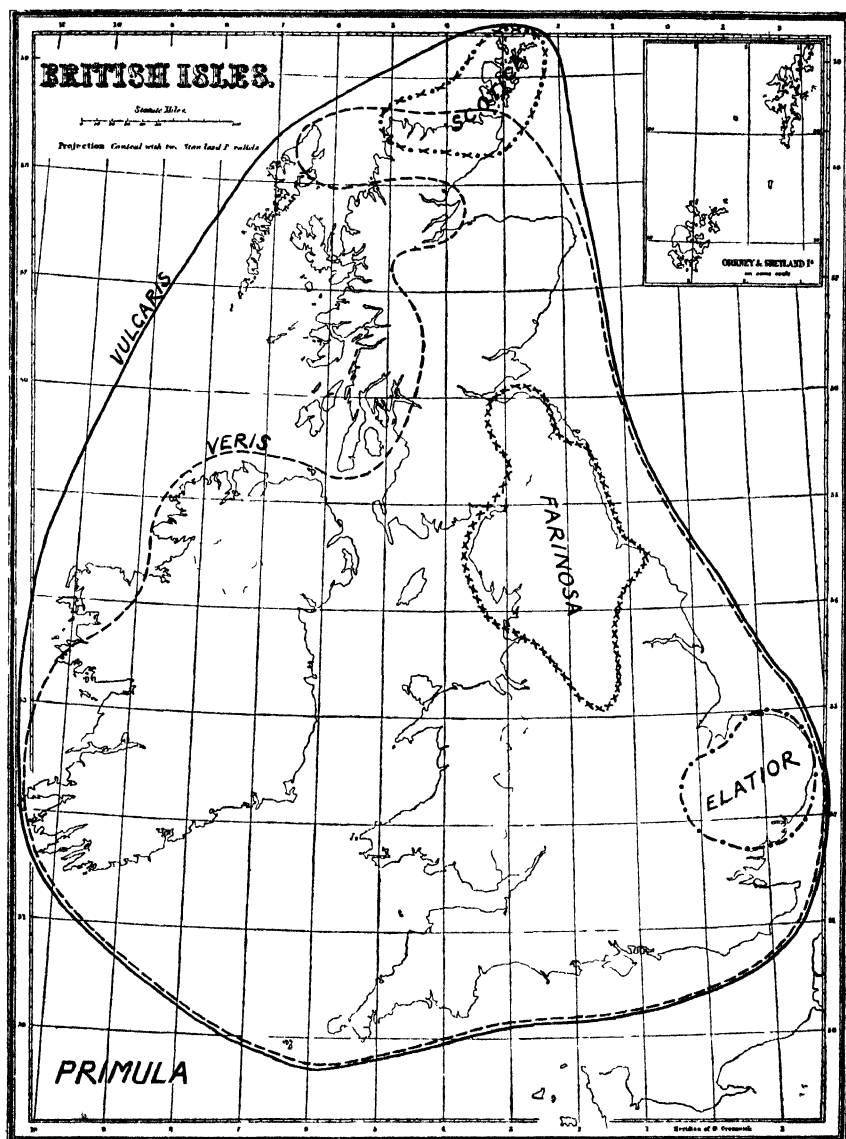


FIG. 52.—Map showing the distribution of the species of *Primula* in the British Isles.

believing that in Pliocene times Britain was part of the continent, joined to what is now western Europe across the southern part of the North Sea and that across this now water-covered area there flowed a greater and longer river Rhine of which in all probability the Thames was a western tributary. With the coming of the ice in the Pleistocene, the drainage of this great river to the north was dammed and the confined water escaped by cutting through what is now the Straits of Dover, thus completely severing Britain from the mainland. It is also supposed that at some later date this strait was again obliterated owing to the elevation of the land in relation to the sea, and that only comparatively recently has the sea once more broken through to give Britain its insularity. That eastern England was indeed at one time part of the basin of the Rhine is supported by the observations of Stomps (236), who finds that some of the plants especially characteristic of East Anglia are equally characteristic of those parts of the continent which presumably formed part of the east side of the basin of this ancient Rhine. But, whatever the details, it is indisputable that great geographical changes have taken place, and it is probably to these that the extinction of so many large mammals is due.

To return to the plants, what is said in Chapter 14 about the glaciations of the Pleistocene points strongly to the fact that, however much the Cromer Forest plants may resemble the present flora, it is impossible to imagine this similarity as due to the persistence of the flora unchanged ever since Pliocene times. During the maximum glaciation, for example, Britain suffered intense ice action, and there is little doubt that most of it, except the extreme southern part, was covered either by ice-caps or glaciers. In addition, there were other less severe glaciations and it seems clear that during some period of the Pleistocene a portion at least of the preglacial flora must have been driven south beyond the confines of the country, and hence that its presence here now must be due to subsequent reimmigration. This broad statement admits of little argument. What is uncertain is the extent to which the early flora was affected in this way, and in particular the proportion of it which was thus destroyed or driven out. On this question there is much controversy and the opposing points of view must be considered with some care.

The problem really turns on two points, first, that of the real extent to which the country was glaciated, and second, the value as indications of climatic conditions of certain plant remains dating from the time of glaciation.

There is at the outset a difficulty in determining the actual extent of the ice at its maximum in that it is not easy to assign a limit to the effect of ice action. The limit of the ice as laid down in most geological accounts is a line joining the Severn and the Thames and passing south of Ireland and it is presumed that north of this line the ice was more or less continuous. But if this was the edge of continuous ice, it seems certain that much of the country further south must have contained numerous glaciers, and the size and number of these would obviously be of great importance. The thickness of glacial deposits but a little north of the Thames suggests that they must have been very extensive, and if so, then the effective limit of ice action must have been considerably further south. It is true that in general there are no glacial deposits in south England, but it is also to be noted that in recent years the occurrence of something of the sort (in one case an actual boulder clay) has been recorded not only from the north coast of Devon (55) but even from the Scillies (12). Another deposit of southern England, the Coombe rock, is also believed by some to owe its origin in part to glacial conditions. All these

remains, however, are slight and it may be accepted that south England was never covered by an ice-cap, although it may have been the site of numerous glaciers. This is the usual state of affairs on the margin of an extensive ice-sheet, as is seen in Greenland to-day, where near the coasts the marginal thinning of the ice, together with the relief of the land, leads to a fringe of glaciers among and between which emerge the unglaciated summits known as "nunataks."

The theory that there were such nunataks not only in southern England but also further north, and that some of the flora found on them refuges in which it was able to survive the effects of the ice, has received considerable attention. Undoubtedly there are considerable areas even in north England which show no signs of ever having been covered with ice. One such large area is in the southern Pennines, and another is in Upper Teesdale. Many of these nunataks, it has been pointed out, are to-day remarkable for the number of rare plants to be found on them. Upper Teesdale, for instance, has several plants which are to be found practically nowhere else in Britain, and some of the British endemic forms (see below) are also restricted to such areas.

The possibility of the survival of members of the pre-glacial flora on unglaciated areas has been discussed with special reference to Great Britain by many geologists and botanists including Blackburn (27) and Raistrick (190), but the theory originated in connection with the investigations of Fernald and others into the flora of the shores of the Gulf of St. Lawrence in eastern North America (see Chapter 8). There occur here in certain places many peculiar species and forms often quite foreign to the region in general and most closely related to other species to be found many hundreds of miles away, and this has been explained on the view that they are ancient types which have persisted for thousands of years and throughout at least part of the glacial period on the unglaciated regions.

The theory is an attractive one, and that it is true to some degree can hardly be disproved, but it is only fair to say that both in North America and Britain the facts can be explained otherwise. In the former, Marie Victorin (159) believes, for instance, that the observed facts may be the result of divergent migration from one more northerly centre. In Britain it has been suggested that the rare and local plants mentioned above are to be regarded not as ancient survivors but as recent arrivals in their respective habitats.

There is also another great objection to the theory of nunatak survival, namely, that if these unglaciated spots were, during the ice ages, peculiarly suitable for the plants concerned, they would almost certainly not be so now, and there seems no reason why they should still be restricted to them when the general conditions of the region have so materially altered.

Another argument used in favour of the view that a considerable proportion of the pre-glacial flora may have survived the glaciations is that to-day warmth-loving plants are often found growing in close proximity to glaciers. Hooker in his *Himalayan Journal* pointed out that the direct distance between the perpetual snows of these mountains and the tropical flora at their base was only about six miles, and more recently attention has been drawn to the occurrence in New Zealand of tree ferns equally near or even nearer to glaciers. These facts are undoubtedly striking, but they afford little indication of conditions in Britain during the Pleistocene. In both cases the ice concerned is the ice of mountain glacier systems and not the ice of continuous ice-sheets centred near the pole, and the difference is fundamental. The ice is present because of the elevation of the land and not because of the refrigeration at sea level of the whole latitudinal zone

in which it is found, and on this account its influence on the climate is extremely local. Not only are polar ice-caps much more extensive but their very presence and persistence indicates minimum climatic values over wide areas, and their effects are felt far beyond their boundaries. To-day there is probably only one part of the world where conditions are at all parallel to those which must have existed in Britain during the Pleistocene. This is Greenland, which can, as a result, support only an arctic flora composed of the most cold-resisting types. There are neither tropical nor even warm temperate species within hundreds of miles of its shores.

On this analogy, at any rate, it is difficult to believe that, if the conditions in Britain during the ice ages were as they have been pictured, the flora can have been anything more than an arctic flora with perhaps an ingredient of a few particularly hardy species of a more temperate character.

Let us now turn to the actual remains of the vegetation of the Pleistocene in this country. Unfortunately these are not very extensive, but there are some at least, and they have been the subject of much argument. This centres chiefly round certain so-called "arctic beds" whose remains have been described from such different parts of England as East Yorkshire, East Anglia, Cambridgeshire (40), the Lea Valley (195), South Devon and the Isle of Wight. From these deposits there have been identified various plants which to-day are associated with arctic floras such as some of the smaller willows, *Betula nana*, *Oxyria digyna*, *Arctostaphylos* and *Ranunculus hyperboreus*, and it has been argued that the presence of these species indicates arctic conditions at the time and place of their deposition, and as a corollary that plants of less arctic character must have had a home much further south. At first sight this seems a reasonable suggestion, but closer investigation reveals difficulties. Wilmott (264) has shown that the species mentioned are generally accompanied by others which are certainly not arctic in type, such as species of *Silene* and *Linum* in the Lea Valley flora, and in addition he is of opinion that some of the identifications are far from satisfactory. Indeed, if the total remains in these various beds are considered without special emphasis on particular species, their arctic character is open to doubt.

Nor are all the floras of the Pleistocene of the same character. In West Sussex, for instance, plants like oak, elder, dogwood and a now exotic maple have been recorded, showing that at some stage of the Pleistocene, presumably during the inter-glacial period that followed the maximum glaciation, quite a temperate flora existed at least in the south of the country.

In short there seems no direct evidence by which the proportion of the pre-glacial flora which was able to persist unharmed in this country during the ice ages can be determined, and it is not surprising that there is a good deal of difference of opinion. Wilmott (266) some years ago expressed the view that in the main the present flora consists either of boreal and montane plants which would scarcely be affected by ice or of common central European plants which in his opinion might have survived south of the Thames, and other botanists have taken up much the same belief. On the other hand, Salisbury (266), Reid (193) and others believe that only the arctic and boreal types can have survived.

Both these views really concern only the commoner and more generally distributed British plants. As will be seen later, there are many species in the flora which are confined even to-day to the warmest and most southerly parts of the country, and there is no suggestion that these can have survived glaciation *in situ*. The statement that the British flora is to be regarded as essentially an immigrant

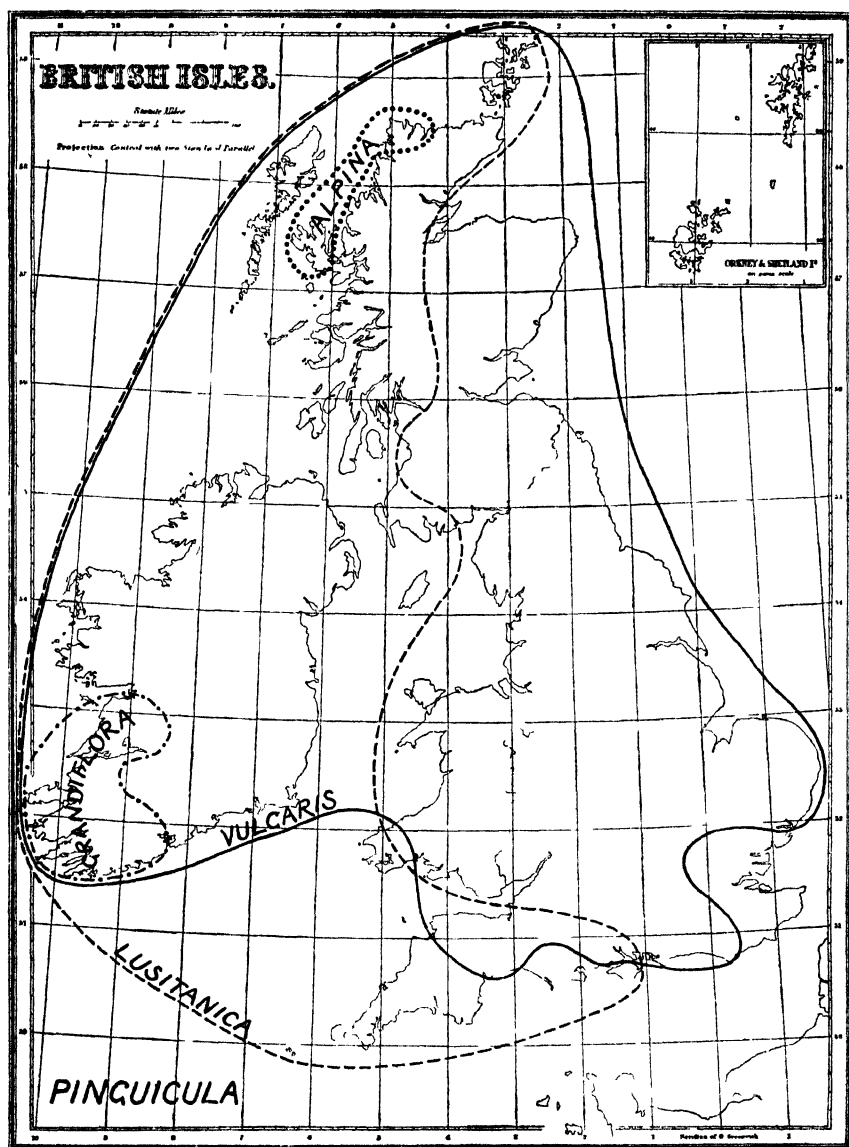


FIG. 53.—Map showing the distribution of the species of *Pinguicula* in the British Isles.

ARCTIC
(glacial).

The sequence of conditions shows, as is only to be expected, a series of increasingly temperate floras following the most recent retreat of the ice, and on the whole this gradual amelioration is unbroken except for the occurrence of a suggested climatic optimum (post-glacial optimum) somewhere at the end of the boreal period. This gradual amelioration is in itself evidence that the immigration and re-immigration of species into the country must also have been gradual, and the relatively great changes which were clearly necessary to re-establish the flora in the condition in which it existed before the ice ages is sufficient demonstration of the effects of the glaciation upon the plant life.

But the building up of the present British flora has not been conditioned by climate alone. For several thousands of years now the country has supported an ever increasing human population, and a proportion of the flora certainly owes its presence to the intentional or accidental influences of human beings. Each of the human waves of invasion which constitute so much of British history has brought with it plants long associated with its peoples in their earlier homes, and each phase of history is reflected in the flora.

From the point of view of its influence on the natural vegetation the history of Britain may be divided into five periods, each of which has had its own effect on the plant life. For many centuries following man's first appearance on our shores the land was inhabited by a succession of relatively primitive communities who were able to make but little headway and impression against the forces of nature. Even agriculture, when it came to be practised at all, was practised on a very simple and restricted scale, and was almost certainly of necessity confined to the more accessible and amenable parts of the country like the chalk and limestones, where little natural vegetation had to be cleared to make way for it, and where on the other hand its effect on the general plant life was least.

This continued until, with the coming of the Romans shortly after the beginning of the present era, the second period began. The Roman occupation lasted for roughly 400 years, and there is no doubt that during that time the internal organisation of the country was raised to a level which it did not again reach for more than a thousand years.

The effect on the vegetation must have been profound, for the Romans brought with them or developed later the tools and technical knowledge which made it possible for them to subdue their environment almost completely. Forests were cleared; swamps were drained; roads were built; and indeed nearly all the activities calculated to modify the natural vegetation were in progress. Agriculture, too, was far more extensively and variedly carried on than before. It is difficult to visualise the condition to which all this must have brought the country eventually, but there is reason to believe that in the south of England, at any rate, the zenith of the Roman period, reached in the third and fourth centuries of our era, must have revealed a countryside not widely different from that of two or three hundred years ago.

Unfortunately for history, but perhaps fortunately for the flora, this standard was not maintained. The waning of the imperial power eventually necessitated the withdrawal of all the legions from Britain. With them went the hope of safety, and from that time the country sank under the plundering of its enemies into a state of collapse and chaos, during which it is certain that the work of the Romans was virtually destroyed. Cities disappeared; forests spread once more; drainage failed and cultivated land degenerated into grassland, thicket and woodland.

This relapse continued, with no doubt some slow improvement, for a very long

time. Not until the Norman period was there even any real political stability, and as far as the vegetation was concerned it can hardly have altered much again until the feudal system which the Normans established gave place, in the course of time, to the manorial system. This was based at least in part on agriculture, and as it became firmly established the vegetation must once more have undergone a slow but steady modification. Whether this was as marked as it had been in the Roman period is doubtful, but it was almost certainly more widespread, and it was probably now for the first time that some of the remoter parts of the country felt the real impress of man and his works.

Although the gradual growth of the population and the development of the country accelerated as time went on, there was no essential alteration that affected the vegetation until the middle of the eighteenth century. Up to that time Britain remained a purely agricultural country.

But about 1750 there was ushered in the period which was destined to see a greater revolution in almost every sphere than any that had gone before it—the age of industrialism and urbanism. Within a space of less than 200 years miles of what was hitherto largely fair and untouched country has become covered, to the utter exclusion of natural vegetation, with the products and achievements of man's hands and brain. The process still goes on. Every year more and more of the country disappears under the insatiable demands of the town and factory, and only in the last decade or two has there been any real indication that a long slumbering public conscience will at last awake and demand a cessation of what is partly senseless and unnecessary destruction.

This latest period is from the plant point of view unlike the rest in that it has been almost entirely destructive. In earlier times what loss there may have been among native plants was probably more than balanced by the introduction of new species, but with industrialism there has been little such compensation except perhaps for a few garden plants which have established themselves among the wild ones. Modern farming does not encourage the weeds which, while a bane to the farmer, are often a joy to the botanist, and in addition there are the depredations of the plant collector who, it may or may not be significant to note, seems to have multiplied with the growth of industrialism.

An interesting attempt has been made to assess the changes which have taken place in the British flora in the last fifty years (265). From it, it would seem that while several species have become extinct more have been discovered by intensive study or collecting, and so the total number is slightly on the increase. At the same time it seems certain that many of the favourite wild plants are far less abundant than previously and are at least in danger of ultimate extinction, not by the processes of unaided nature but by the thoughtless or deliberate actions of their admirers.

Such is the story of the development of the British flora down to the present day. Its long and eventful history has been told in outline, and we have seen that it is now an assemblage of species moulded and modified in many different ways and by many different events and processes. This assemblage and the way in which it is distributed within the country must now be discussed.

The scientific study of the distribution of British plants may be said to date from the work and writings of Hewett Cottrell Watson, who devoted a long and active life to it. Certain earlier writers had touched upon the subject, but their writings were merely lists of the localities of some of the rarer species designed primarily for the convenience of collectors.

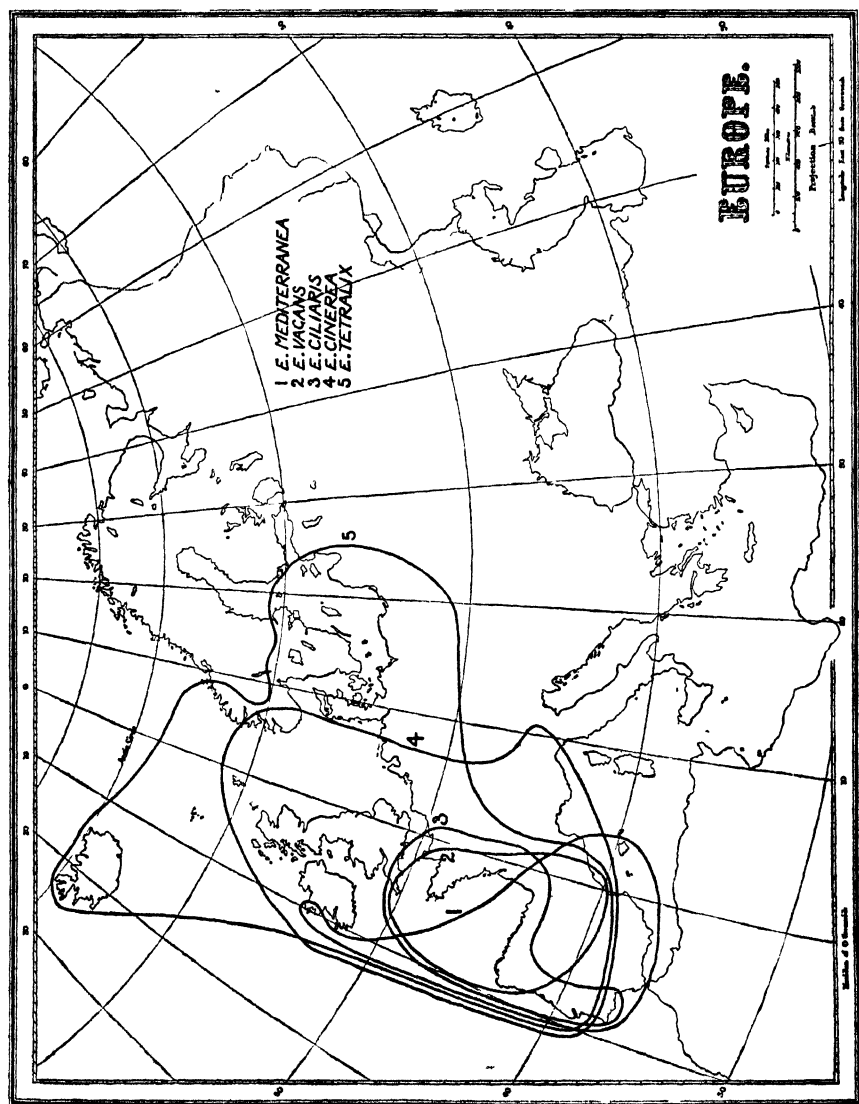


FIG. 54.—Map showing the distribution of the species of *Erica* in Western Europe.

Watson's first two works (253, 254) appeared in 1832 and 1835 respectively, but it was between the years 1847 and 1859 that there appeared his great four-volume work the *Cybele Britannica* (255), in which were brought together all the known facts concerning the geography of the species comprising the British flora. In the *Cybele* Watson analysed and arranged the British plants according to several methods which have ever since remained the basis for the geographical study of British plants, and they may therefore be properly considered here at some length.

He dealt first with the actual ranges of the species in Great Britain by dividing the region up into eighteen provinces and noting in which of them each plant occurred. The provinces were based chiefly on major topographical features and were :

- | | | |
|----------------|----------------|---------------------|
| 1. Peninsula | 7. North Wales | 13. West Lowlands |
| 2. Channel | 8. Trent | 14. East Lowlands |
| 3. Thames | 9. Mersey | 15. East Highlands |
| 4. Ouse | 10. Humber | 16. West Highlands |
| 5. Severn | 11. Tyne | 17. North Highlands |
| 6. South Wales | 12. Lakes | 18. North Isles |

The actual limitation of the provinces was chiefly by counties.

Next he classified the species according to the altitude at which they grow, recognising and characterising six zones :

- | | | | | |
|----------------|---|---|---|--|
| Super-arctic | . | . | . | <i>Salix herbacea</i> without <i>Calluna</i> . |
| Mid-arctic | . | . | . | <i>Calluna</i> without <i>Erica</i> . |
| Infer-arctic | . | . | . | <i>Erica tetralix</i> without <i>Pteridium</i> . |
| Super-agrarian | . | . | . | <i>Pteridium</i> without <i>Rhamnus</i> , etc. |
| Mid-agrarian | . | . | . | <i>Rhamnus</i> without <i>Clematis</i> , etc. |
| Infer-agrarian | . | . | . | <i>Clematis</i> , etc. |

The arctic region was that above the limits of cultivation and the agrarian region the lower agricultural levels.

This altitudinal classification although of considerable interest was not on the whole very satisfactory because of the innumerable complicating factors. It is still occasionally referred to, but is the one part of Watson's work which has virtually become obsolete.

A third classification is perhaps the most important of all, and marked a very definite step forward in the geographical conception of the British flora. This was the recognition of seven types according to the generalised distribution of the species within Great Britain (figs. 52, 53). Actually Watson had referred to such types in one of his earlier books, but here in the *Cybele* they were described in more definite fashion as :

1. British type Plants occurring in all or nearly all the provinces of both England and Scotland.
2. English type Plants predominantly English in distribution, especially southern and becoming rare towards the north.
3. Scottish type Plants predominantly Scottish in distribution, especially northern and becoming rare towards the south.
4. Highland type Plants confined to the mountain regions of England and Scotland.



Plate 16 Mangrove Vegetation on the Coast of Lower California

(from Karsten & Schenck, Vegetationsbilder)

5. Germanic type Plants characteristic of the east part of England.
6. Atlantic type Plants characteristic of the west and south-west parts of Britain.
7. Local or doubtful type.

Mention must be made at this point of Forbes' (82) publication in 1845 of a very similar series of types or, as the author called them, "floras." We need not be concerned whether or not, as has been stated, this work of Forbes' was in fact a plagiarism of Watson's earlier work in which his types had first appeared. The important point is rather that Forbes not only listed his floras or, as we should call them to-day, "floristic elements," but also explained them on the grounds that they represented the stages and directions of the immigration of plants into this country following the ice ages. For this reason Forbes' work, even if not altogether original, cannot be ignored, and will be referred to again later.

To return to the *Cybele*. Watson next dealt with the British plants according to their status in the country, that is to say, according to their mode of origin. This question of status is a very thorny one, largely because in many cases the truth can never now be discovered, but it is also a very interesting one and helps very much in appreciating our flora properly. Here again, Watson's work has stood the test of time and his classification, which is as follows, is substantially that still in use to-day.

The first and most important category is that of the "native" species. These are the plants whose presence in the country has nothing to do with human action either direct or indirect. Many of them have no doubt existed in the country much longer than man himself and for this reason they have been described as botanical aborigines or, as the phrase goes, "aboriginal possessors of the soil." At the same time they certainly include some recent immigrants. It is to these native species that the natural vegetation of the country is almost entirely due.

The next category comprises all these species which owe their presence indirectly to man's activities. They are in short the weeds of cultivation which in absence of agriculture would find no home here. These plants Watson called "colonists."

Next come the plants which owe their presence to the direct action of man, that is to say, which have been introduced deliberately for purposes of cultivation but which have subsequently escaped from these surroundings and established themselves among the natural vegetation as a permanent feature of it. Such are called "denizens."

Lastly, there are the species which are constantly introduced by accident in the form of seeds and fruits, which grow for one or more summer seasons but which do not normally reproduce and whose presence is therefore transitory. They are found only in disturbed ground and play no part in the natural vegetation. No doubt on the grounds of their foreign origin these plants were called "aliens," but the more recent terms "casual" and "adventive" are perhaps to be preferred.

Finally Watson classified the flora on what we should now call an ecological basis into the following groups according to habitat:

1. Pratal Plants of meadows.
2. Pascual " " less rich pastures.
3. Ericetal " " moors and heaths.
4. Uliginal " " swamps and bogs.
5. Lacustral Submerged or floating aquatics.
6. Paludal Plants of marshy places.
7. Inundatal " " places liable to winter flooding.

8. Viatical . . .	Plants of disturbed ground.
9. Agrestal . . .	„ „ cultivated ground.
10. Glareal . . .	„ „ dry exposed ground.
11. Rupestral . . .	„ „ walls and rocks.
12. Septal . . .	„ „ hedges.
13. Sylvestral . . .	„ „ woods and shady places.
14. Littoral . . .	„ „ the seashore.

By the combination of these classifications Watson was able to give a very complete picture of the distribution of each British plant not merely in terms of its actual geographical range but in terms of geographical range, altitude, status and ecology, and a list of the British plants embodying this information is the main part of the *Cybele*.

In 1860 there appeared the first part of a supplement to the *Cybele* and in 1868-70 the three volumes of the *Compendium of the Cybele Britannica*. In these works Watson made two further great advances in British plant geography. In the first place he replaced or elaborated his eighteen provinces by dividing the whole of Britain into 112 vice-counties, and in the second he discussed for the first time the extra-British ranges of the members of the British Flora. His system of vice-counties is still in full use, and more and more attention has come to be paid to the wider distribution of British plants.

Finally, in 1873-4, Watson published his last work, the two volumes of his *Topographical Botany* (256), which provided in tabulated form a summary of the known distribution of British plants. Its concise and convenient form has given to *Topographical Botany* a popularity which in comparison with the *Cybele* it scarcely deserves, and it has been kept up to date ever since by a second edition and by supplements.

Most recently Druce's *Comital Flora* (62) is, as its author states, mainly a modern revision of *Topographical Botany* with Ireland also included.

Regarding this latter point Watson did not deal with Ireland in either the *Cybele* or *Topographical Botany*, but this gap has long been filled by corresponding publications by Colgan and Scully (47) and by Praeger (184).

Any work which consists of the compilation and collection of records which are ceaselessly being made can never possess finality, and since Watson's day botanists have repeatedly revised or added to his work in detail, but it is a remarkable tribute to him that during a time of such rapid scientific advance the main outlines of his studies remain practically in the form in which he stated them. Some aspects have received more attention than others but the framework remains.

This sketch of Watson's work has had two functions: it has given an account of the origin and development of the study of the geographical features of British plants, and it has also indicated the main ways in which that study has been conducted. With it as a background we may go on now to a brief consideration of the present position of these studies and to illustrate them by the examples which it would have been out of place to mention above.

Since Watson's time research into the distribution of British plants has continued mainly along three lines. The first is in fact the whole subsequent growth and development of the science of plant ecology or the study of the plant in relation to its environment, and while it would be extravagant to hail Watson as the first plant ecologist there is, nevertheless, a clear forecast of the study of ecology in his classification of plants according to the kinds of habitat they occupy. Since his

day ecology has developed so far and so wide that it has become a subject of its own, ranking with, and complementary to, the subject of plant geography in the narrower sense which deals with the spatial relations rather than with the physiological relation of plants to the earth that bears them. Since this book is devoted to plant geography in this narrower sense, plant ecology falls outside its scope and further information concerning this particular subject must be sought elsewhere. Nevertheless it must be borne in mind that this sharp demarcation of interests is largely made inevitable by the exigencies of convenience. It is not a natural separation, and the two subjects of plant ecology and plant geography are inter-related at almost every point.

The second line of development in British plant geography has been the further study of the classification of species according to their distribution *within* the country itself, an extension as it were of Watson's "types" and Forbes' "floras", and the third line has been the elaboration of the classification according to the distribution of the species *outside* Great Britain. The present position regarding both these must now be considered.

In doing this it is necessary to write largely in terms of numbers. As was made clear earlier, numbers may mean little or much and must not be regarded too seriously, but without them it is almost impossible either to make comparisons with other floras or to demonstrate the comparative importance of different components. They also have another value in that they illustrate very vividly the extent to which our conceptions of the flora depend upon individual opinions, a limitation which cannot entirely be surmounted.

The differences which exist in the various estimates of the size, in number of species, of the British flora are chiefly due to two difficulties. The first lies in deciding to what degree the recognition of small species or "microspecies" should be carried and the second in deciding exactly what plants deserve to be considered as members of the established flora.

As a general rule the more a genus is studied the more obvious become the differences between the individuals which comprise it, with the result that more and more species tend to be recognised in it, and these species to become smaller and smaller in value and distinction. For example, the blackberries to the everyday field botanist appear to belong all to one variable species but to the specialist who has particularly studied them this one variable species is regarded as comprising a large number of separate microspecies. Similarly, in the genus *Hieracium*, the non-specialist regards the British forms as representing about half a dozen species, but the specialist may recognise among them as many as 250.

The fact is that the species is not a standard measure and varies according to the conception of the individual. It is therefore really impossible to determine how many species there actually are in the flora, and all that can be done is to arrive at some conclusion that will give a reasonable picture and estimate of the number of apparently different plants or, to use a scientific term, *phenotypes* present. How difficult even this is can be shown by a consideration of some actual estimates.

As regards status, it is with the casuals that the difficulty lies. Are any of them, and if so which of them, to be treated as definite members of the British flora? Although it is easy to define them as a class in general, it is not always easy to say exactly which species fall into this category. Some are more firmly established than others and some have almost the rank of colonists or denizens. For the most

part, casuals are not regarded as members of the flora proper because they are not permanent and because they occupy no niche in the general vegetation, but some authorities include them and thereby increase the length of floral lists very considerably.

The effects of these two difficulties are best seen by referring to particular works on the British flora. One of the most satisfactory accounts of British plants is Hooker's *Student's Flora* (130) in which about 1,300 species are listed. Bentham and Hooker's *Handbook* (14, 81), which is perhaps the most familiar of all our Floras, gives about the same number. In both these works casuals are for the most part excluded. At the other extreme Druce's *British Plant List* (61) enumerates no fewer than 4,250 species, casuals included.

Fortunately we can resolve this disparity to some extent. There is practical agreement that the figures of Hooker and of Bentham and Hooker are too small, and that many worthy species have not been recognised in them, and this opinion has been implemented by the recent publication of what is in fact an appendix to these works enumerating some 500 additional species (33). Examination of Druce's lists shows that no fewer than 1,750 casuals are included, and if these are cut out the total drops to something more than 2,500. Even this includes an extreme recognition of microspecies.

Here we can gain assistance from various other floras not yet mentioned. Babington (9) for instance, gives 2,250 species including many *Rubi* and *Hieracia*. Hayward (115) gives some 1,650 excluding microspecies of *Rubi* and *Hieracia*. The *London Catalogue* (150) gives about 2,250 but includes large numbers of microspecies in the genera mentioned.

From this maze of figures it is possible to make some generalisation. It seems fairly clear that most authorities regard our flora as composed of about 1,750 species if certain microspecies and all casuals are excluded; as composed of about 2,250 species if the microspecies are included; and of anything up to 4,500 species if all possible casuals are included. For our present practical purpose then we shall be reasonably justified in regarding the flora as consisting of about 1,750 well-defined species.

The next question is the proportion of the different status categories in this total. Here again it is difficult to reach conclusion, but, making a synthesis of various opinions, it would appear that of the 1,750 probably some 1,250 deserve the title of native. About 250 are to be regarded as denizens, leaving a rather indefinite figure, not exceeding 250 and probably rather less, for colonists.

For statistical purposes only species are taken into account, but many species actually occur in two or more well-marked subspecies or varieties. In addition there is a considerable number of inter-specific hybrids, and certain genera such as *Salix*, *Rumex* and *Rosa* are particularly rich in them.

With regard to casuals, only one further point need be mentioned here. Fresh species are always being introduced into the country, and as there is no means of telling which of previous entrants still persist, the total number of recorded casuals is always increasing. This is the chief reason why every fresh estimate which includes such plants tends to contain more species. These estimates represent, however, not the condition of affairs at any one time but the total records over a long period.

The term British as applied to the flora includes not only Great Britain and Ireland but also the Channel Islands. The last named, however, are included solely on political grounds, the flora actually being far more French than British

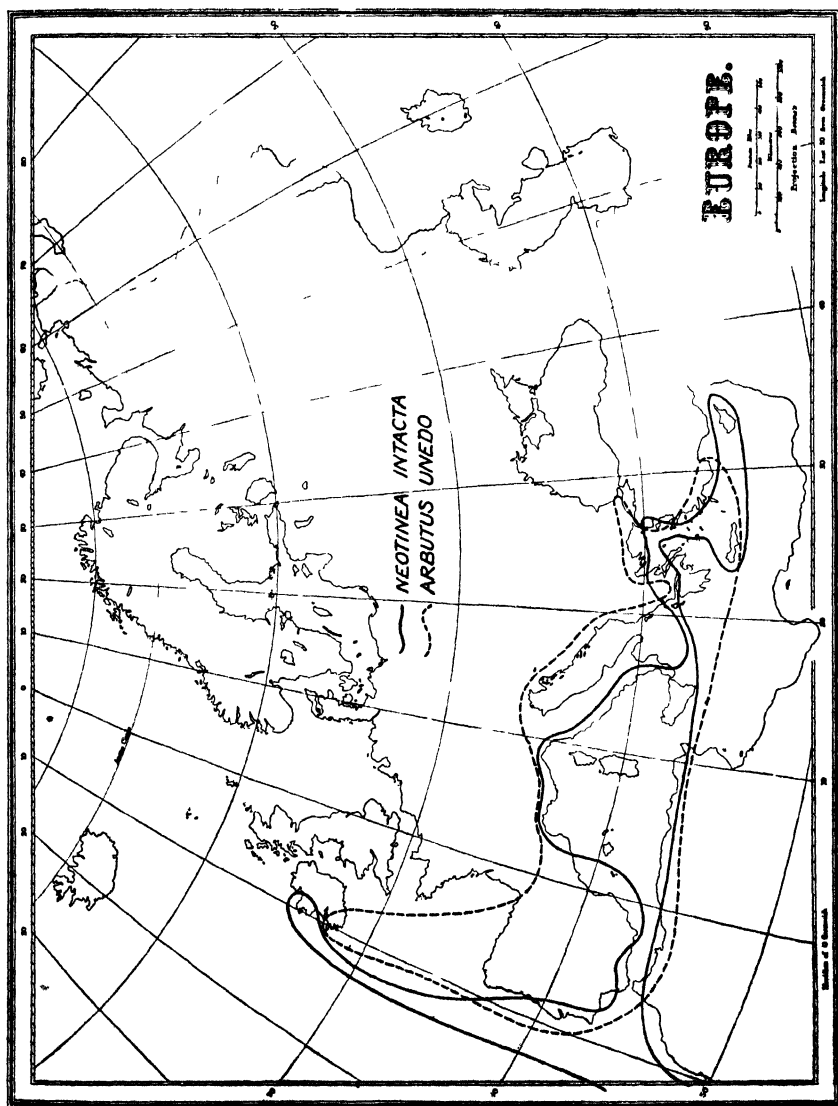


FIG. 55.—Map showing the distribution of *Neotinea intacta* and *Arbutus unedo*. The former extends to Macaronesia.

in character. They may therefore be excluded except for special mention. It may be noted that some twenty species are found in these islands only and not in the British Isles proper.

It happens that the distributions of plants in Britain and in Ireland respectively have nearly always been treated as two separate problems, and it is appropriate therefore to treat them so here, and it is convenient to begin with Britain. The distribution of plants in Britain is generally expressed in terms of the 112 vice-counties into which Watson ultimately divided the country, and this is probably as good a way of conveying their ranges as can be suggested.

The *London Catalogue* (150), as well as one or two other works, summarises the information available in a convenient way, and the following table is taken from that work.

About 7 per cent. of all species are recorded from every one of the vice-counties.

"	10	"	"	"	"	"	"	100-111
"	5	"	"	"	"	"	"	90-99
"	5	"	"	"	"	"	"	80-89
"	5	"	"	"	"	"	"	70-79
"	5	"	"	"	"	"	"	60-69
"	5	"	"	"	"	"	"	50-59
"	5	"	"	"	"	"	"	40-49
"	6	"	"	"	"	"	"	30-39
"	7	"	"	"	"	"	"	20-29
"	12	"	"	"	"	"	"	10-19
"	22	"	"	"	"	"	"	2-9
"	6	"	"	"	"	"	"	only 1

The main fact which emerges from these figures is that the species in total show every degree of range from the minimum to the maximum. Actually the figures given are probably all on the low side, since our knowledge of plant distribution even in this country is still far from complete. For instance, many of those in the second line will probably be ultimately discovered in the one or few remaining counties. On the other hand, the comparatively large figures towards the bottom of the table are caused by recently recognised species whose ranges are still largely problematical.

The plants recorded from all vice-counties include, as might be expected, many of the commonest and most familiar, as, for instance, *Achillea Millefolium*, *Bellis*, *Capsella*, *Cerastium vulgatum*, *Cirsium arvense*, *C. palustre*, *C. vulgare*, *Corylus*, *Hedera*, *Juncus conglomeratus*, *J. effusus*, *Lotus corniculatus*, *Prunella vulgaris*, *Ranunculus acris*, *R. bulbosus*, *R. repens*, *Rumex Acetosa*, *R. Acetosella*, *R. crispus*, *R. obtusifolius*, and *Taraxacum*, together with such grasses as *Briza media*, *Dactylis*, *Holcus lanatus*, *Lolium perenne*, *Poa annua* and *P. pratensis*. Also included are various species distinctly less abundant but nevertheless thus completely distributed. Among these are *Achillea Ptarmica*, *Alopecurus geniculatus*, *Galeopsis Tetrahit*, *Hydrocotyle*, *Linum catharticum*, *Lychnis Flos-cuculi*, *Molinia caerulea*, *Myosotis versicolor*, *Oxalis Acetosella*, *Ranunculus hederaceus* and *Thymus Serpyllum*.

The species confined to only one vice-county include, as has been indicated, a number of microspecies whose real distribution is still uncertain, but there are others about which there is no doubt. Not only so, but they are sometimes recorded only from a single spot. This is true of *Cotoneaster* on the Great Orme; *Dianthus gratianopolitanus* (*caesius*) at Cheddar; *Saxifraga cernua* on Ben Lawers;

Arenaria uliginosa on Widdybank Fell ; *Scorzonera humilis* from one or two spots in Dorset ; *Lloydia* from a rock face in the Snowdon Range, and three species of *Trifolium* from the neighbourhood of the Lizard Point.

These latter species are to be regarded as among our rarest plants, but it is perhaps more accurate to call them local rather than rare. They may and sometimes do occur within their limited habitats in considerable quantity, while there are other species which, though more widespread, have been seen only in very small numbers and at long intervals of time. It is to these latter that the word rare more appropriately applies. An extreme instance of rarity in this sense is afforded by the orchid *Epipogium aphyllum*, of which in the last hundred years no more than about half a dozen individuals have been noted in three or four different and widely separated localities. Several other orchids are similarly but less conspicuously rare in this strict sense.

In view of what has just been said it would be interesting to arrange the vice-counties in order according to the total number of species recorded from each, but it is difficult to do this sufficiently accurately to be of value. It is clear, however, that the richest vice-counties are those in the extreme south-west and south-east of England, namely Cornwall, Sussex and Kent, and that from these points the richness decreases fairly regularly northward and westward. In short, there are most species in those parts of England nearest to the Continent, a feature which, in view of the glacial and post-glacial history of the flora, is only to be expected.

That even to-day there is much to be learnt about the distribution of species in Britain has lately been demonstrated vividly. Among the species long regarded as extremely restricted in their range are *Cicendia pusilla* from the Channel Islands only ; *Juncus mutabilis* (*pygmaeus*) from Cornwall only ; and *Juncus capitatus* from Cornwall and Anglesey. Within the last few years, however, all three of these have been recorded by Heslop Harrison (119, 120, 121) from apparently natural habitats on islands of the west coast of Scotland. Another instance concerns an Irish plant, *Arbutus Unedo*, which Praeger (188) has lately recorded as native from Sligo, no less than 160 miles further north than its most northerly previously known station.

The question of the comparative distribution of species over Britain can best be dealt with by reference to the types of Watson described above. The percentages of these types among British plants is roughly :

1. British type	44 per cent.
2. English type	30 "
3. Scottish and intermediate type	8 "
4. Highland type	5 "
5. Atlantic type	5 "
6. Germanic type	8 "

The British type obviously will include all the plants found in all the vice-counties as well as many not so completely distributed. The disparity between 2 and 3 is due partly to the fact that the majority of the plants found in a medium number of vice-counties fall under 2. It may also be said here that according to most estimates only some seventy species are found in Scotland and not in England. The Atlantic and Germanic types contribute largely to the greater richness of the flora in the extreme south which has already been noted.

The general nature of the flora of Ireland cannot be better described than by

quoting the remarks in the introduction to the second edition of the *Cybele Hibernica* (47). The authors there say that "Viewed as a whole, the flora of Ireland may be regarded as an incomplete English flora, as this in turn may be regarded as an incomplete west European or French flora. It is in the species which it lacks that the Irish flora chiefly differs from the English; and the vast majority of the English plants which are absent from Ireland are common or widespread in western continental Europe."

According to most authorities the number of species in Ireland is about 70 per cent. of the number in England, but they include an appreciable group not found in the latter country. Praeger (187) mentions the following as being definitely of this type, namely:

<i>Arbutus Unedo</i> (fig. 55)	<i>Neotinea intacta</i> (fig. 55)
<i>Arenaria ciliata</i>	<i>Pinguicula grandiflora</i>
<i>Daboecia cantabrica (polifolia)</i> (fig. 56)	<i>Saxifraga Geum</i> (fig. 56)
<i>Erica Mackaiana (Mackaii)</i> (fig. 54)	<i>Saxifraga spathularis</i>
<i>Erica mediterranea</i> (fig. 54)	<i>Sisyrinchium Bermudiana (angustifolium)</i>
<i>Inula salicina</i>	<i>Spiranthes gemmipara</i>

To these are perhaps to be added the following problematical and possibly endemic forms:

<i>Alchemilla colorata</i>	Five species of <i>Saxifraga</i>
<i>Arabis Brownii</i>	Three species of <i>Hieracium</i>
<i>Orchis kerryensis</i>	
<i>Orchis occidentalis</i>	
<i>Orchis traunsteinerioides</i>	

British species absent from Ireland are:

<i>Astragalus Glycyphyllos</i>	<i>Lathyrus sylvestris</i>
<i>Chrysosplenium alternifolium</i>	<i>Ononis spinosa</i>
<i>Convallaria majalis</i>	<i>Paris quadrifolia</i>
<i>Genista anglica</i>	<i>Scabiosa columbaria</i>
<i>Helictotrichon (Avena) pratense</i>	

Among species common in Britain but rare in Ireland are:

<i>Adoxa Moschatellina</i>	<i>Geranium pratense</i>
<i>Calamagrostis Epigejos</i>	<i>Hypericum hirsutum</i>
<i>Corydalis claviculata</i>	<i>Ornithopus perpusillus</i>
<i>Filipendula hexapetala</i>	<i>Teesdalia nudicaulis</i>
<i>Galium Cruciata</i>	<i>Trollius europaeus</i>

Conversely, *Lathyrus palustris*, *Pinguicula lusitanica* (fig. 53), *Rhynchospora fusca*, *Rubia peregrina* and *Utricularia intermedia* are more common in Ireland than in Britain.

For distributional purposes Ireland is divided into forty vice-counties which actually correspond more or less to the political counties. Considering the smaller size and greater homogeneity of Ireland, it is not surprising to find that the number of completely distributed species is proportionately much greater than in Britain. About 250 species are found in all the vice-counties and, also as might be expected, these include nearly all the species which are completely distributed in Britain. The additional species are chiefly of the sort that reflect one of the main ecological features of Ireland, namely, the prevalence of various kinds of aquatic habitats.

This is well shown in the case of the genus *Carex* of which no fewer than fourteen species are completely distributed compared only with four so ranging in Britain.

On the other hand, the number of species occurring in only one vice-county is small, about forty in all, of which some seventeen are microspecies of *Rubus* and *Hieracium*. This figure gives a percentage of 4 as compared with 6 in Britain, but these figures have not much significance.

The concentration of species in the south-east of England and also several peculiarities of the Irish flora have been discussed and demonstrated by Matthews in a series of papers designed to throw light on the paths by which the bulk of the British plants re-entered the country after the glaciation. Matthews argues that the more or less completely distributed British plants, those which occur in nearly all the vice-counties, are not likely to reveal much in this direction, and confines his attention to those which have a markedly narrower range.

In his first paper (162) he analyses that element of the flora consisting of species found only in England and Wales. These he estimates to number 266, and he shows very clearly that they are concentrated in the coastal counties from Dorset to Norfolk, and that this concentration decreases more or less regularly westward and northward. He further shows by inset maps that the area of greatest concentration of these plants outside Britain is in France, where over 90 per cent. of them are to be found.

In a second paper (163) he deals with the 105 species found, in the British Isles, only in England and Scotland. These he finds fall into two almost equal groups, a boreal and a southern, concentrated respectively in Scotland and in the eastern half of England, especially the south-east. Outside Britain he finds the boreal group to be concentrated in Scandinavia, Germany and France, and the southern group in France and Spain.

In his third paper (164) Matthews deals with the Anglo-Irish element of the flora. He refers first to the twenty or so species found only in Ireland, and shows that they belong almost entirely to a south European stock concentrated on the continent in northern Portugal and Spain.

A second, larger, group of sixty-eight species occurring in Ireland and England he shows to have very much the same distribution as was the case of the English plants, namely, a concentration in the coastal counties from Devon to Norfolk together with a concentration in west and south-west Ireland. These plants again are like the English element in that their continental area of concentration is in France.

Taking the three papers together Matthews concludes that the non-boreal element of the British flora, which is the part with which the papers deal, may have begun to re-immigrate into the country directly from south-west Europe and that this was the oldest or first migration, but that very soon the centre of dispersal on the continent moved eastwards to the neighbourhood of France. The migration from this direction he considers to have been a very prolonged one and to account for the preponderance of French and central European species in our flora.

So far our attention has been confined to the distribution of species within the British Islands, but the members of the British flora must next be considered in the light of their distribution outside these countries.

This at once raises the question of British endemics. Are there any species occurring in the British Isles that occur nowhere else and which are therefore

peculiar to them? The answer depends entirely on what we reckon as species. If by the term we mean units of the size, let us say, of those in Bentham and Hooker's *Handbook*, namely, average or large species, then the answer is probably that there are none. If, on the other hand, we take into account small species, then the answer is that a small number are found only in the British Isles. This in one way is quite a sufficient statement, because it illustrates the main point, which is that the peculiar element in our flora is almost non-existent compared with the peculiar element in most other floras of the world.

Wallace (251) gives one of the earliest and most lengthy surveys of endemic British plants. His list, which was compiled by Bennett, includes no fewer than seventy-two microspecies and varieties, but many of these must certainly be excluded. Indeed Hooker, in comments on this list, reduces it to one absolutely endemic species, *Potamogeton lanceolatus* (now known to be a hybrid), and some fifteen varieties.

Wilmott (264) has discussed the matter at some length but does not give a definitive list. It would appear, however, from his remarks that the genera *Arabis*, *Cochlearia*, *Fumaria*, *Limonium* (*Statice*) and *Ulmus* all contain one or more endemic forms which have at some time or other received specific rank, and that in addition many microspecies of *Rubus*, *Rosa*, *Hieracium*, *Euphrasia* and *Thalictrum* are also unrecorded elsewhere.

Salisbury (207) believes that there are fewer than twenty-five endemics including varieties, and Matthews is of much the same opinion. As has been seen, some of these reputed endemics are confined to Ireland.

The first classification of British plants according to their ranges outside this country, and particularly on the continent, was made by Forbes (82) in 1845. He recognised five elements or sub-floras which he believed to represent as many distinct immigrations into the country subsequent to the Pleistocene. They were:

1. Iberian or Asturian :
species found, on the continent, in the north of Spain.
2. Armorican or Gallican :
species chiefly of the Channel Islands and western France.
3. Kentish :
species found particularly in north and north-eastern France.
4. Scandinavian or Boreal :
species representing northern and subarctic floras.
5. Germanic :
species related to those of central and west-central Europe.

Since Forbes' day repeated attempts have been made to improve and amplify this classification, and it would be impossible to deal with these in detail. Matthews (165), however, has brought the whole subject up to date in a single comprehensive paper, and we cannot do better than refer to this at some length.

Matthews treats the native or naturalised flora as comprising about 1,500 species, and divides them according to their extra-British ranges into fourteen groups or elements to which is to be added a small assembly of endemics. This classification is very detailed and can really only be properly appreciated in the original, but for our present purposes, and in order to facilitate a rapid survey, it may be condensed and rearranged as follows :

1. Wide element :
Species found at least throughout the northern temperate regions 205 species.
2. Eurasian element :
Species found generally distributed through Europe and temperate Asia 480 species.
3. European element :
Species generally distributed throughout Europe
130 species.
4. Southern element :
Species whose continental range is predominantly more southerly than this country . . . 315 species.
 - a. Continental southern element :
Species of south and central Europe 127 species.
 - b. Oceanic west European element :
Species found almost exclusively in western (Atlantic) Europe 76 species.
 - c. Oceanic southern element :
Species found chiefly in south Europe and western Europe, including the Mediterranean region 74 species.
 - d. Mediterranean element :
Species whose ranges are centred in the Mediterranean region 38 species.
5. Northern element :
Species whose continental range is predominantly more northerly than this country . . . 142 species.
 - a. Continental northern element :
Species whose main European range is central and north, but including some circumpolar species
91 species.
 - b. Oceanic northern element :
Species characteristic of north-west Europe, but some having a connection with north-east America
26 species.
 - c. Northern montane element :
Species of north Europe reappearing on mountains further south 25 species.
6. Continental element :
Species characteristic of central Europe, generally extending east through Russia into Asia . . 82 species.
7. Arctic-alpine element :
Species characteristic of the arctic or subarctic regions or exclusively alpine 145 species.
 - a. Arctic-subarctic element :
Exclusively northern species . . . 30 species.
 - b. Arctic-alpine element :
Northern species also on southern mountains
106 species.
 - c. Alpine element :
Species of the central European mountains
9 species.

Even in this somewhat simplified form the classification is complex, as is necessarily the case, and it is well to emphasise its more salient features.

It will be seen that the first three elements, comprising some 55 per cent. of the total flora, make up what may be called the expected proportion of the flora. That is to say they contain plants likely to occur merely in virtue of the country's position as part of the northern temperate continent of Europe.

The remaining elements are on most counts of greater interest, because it is in them that we are most likely to find indications of floral history. Matthews discusses them in special detail and brings out many important points, but attention may be concentrated on certain of them.

No portion of the British flora has received so much attention as that which comprises the species which are confined to south-west England and/or Ireland and which, outside this country, are more or less restricted to the Atlantic coast of south-western Europe and/or to the Mediterranean region. The fact that these do not all fall into one of the groups above simply indicates that their continental distribution varies, as Matthews has shown, so that they can be divided into three (4 *b*, *c* and *d*). They have in common one all-important feature, namely that the British part of their total ranges is much further north than the rest. As a whole these plants may be called "Atlantic," but the most noteworthy examples of them form an assemblage which is usually referred to as the "Lusitanian" element in our flora, for the reason that outside our boundaries the species are more or less restricted in range to that part of the Iberian Peninsula. For example, *Saxifraga Geum* (fig. 56) and *S. umbrosa* are, outside Ireland, found only in the Pyrenean region, so that their occurrence in the former is far to the north of the rest of their distribution. Other species are less extreme in that they occur also in various parts of the west coast of France.

These "Atlantic" species in general and "Lusitanian" species in particular have been studied by many botanists. Stapf (234) has given a long account of them, and Praeger (186, 189) has more recently resurveyed the facts and theories concerning them.

The great question is how and when these plants, and especially the Lusitanian species proper, reached our shores. They are to-day found only in those parts of the islands where the conditions are least rigorous, and it seems perfectly certain that, whatever may be true of other species, these plants at least cannot have survived the Pleistocene in their present positions. This being so, they are presumably among the post-glacial immigrants. But whatever the changes in land and sea may have been since the Pleistocene, there is no suggestion that they involve any linkage of Ireland with Britain or of south-west England (and much less Ireland) with France, so that if these plants are indeed relatively recent immigrants, they must have crossed considerable areas of sea.

The problem has been so often debated without conclusion that it seems presumptuous to suggest that its difficulties have been overestimated, but this seems to be the case, for the following reasons.

The actual occurrence of these plants in south-west England and Ireland proves that their climatic and edaphic requirements are different from those of the generality of British plants only in so far as the conditions of south-west England and Ireland differ from those of the rest of the country. That is to say they are present within our boundaries because there are spots therein in which they can find a congenial home and the conditions they need.

Secondly, the separation of Ireland from Britain certainly antedates the Pleistocene, during which the whole of Ireland is said to have been ice-bound, and hence the present Irish flora must have re-immigrated since, and in doing so must

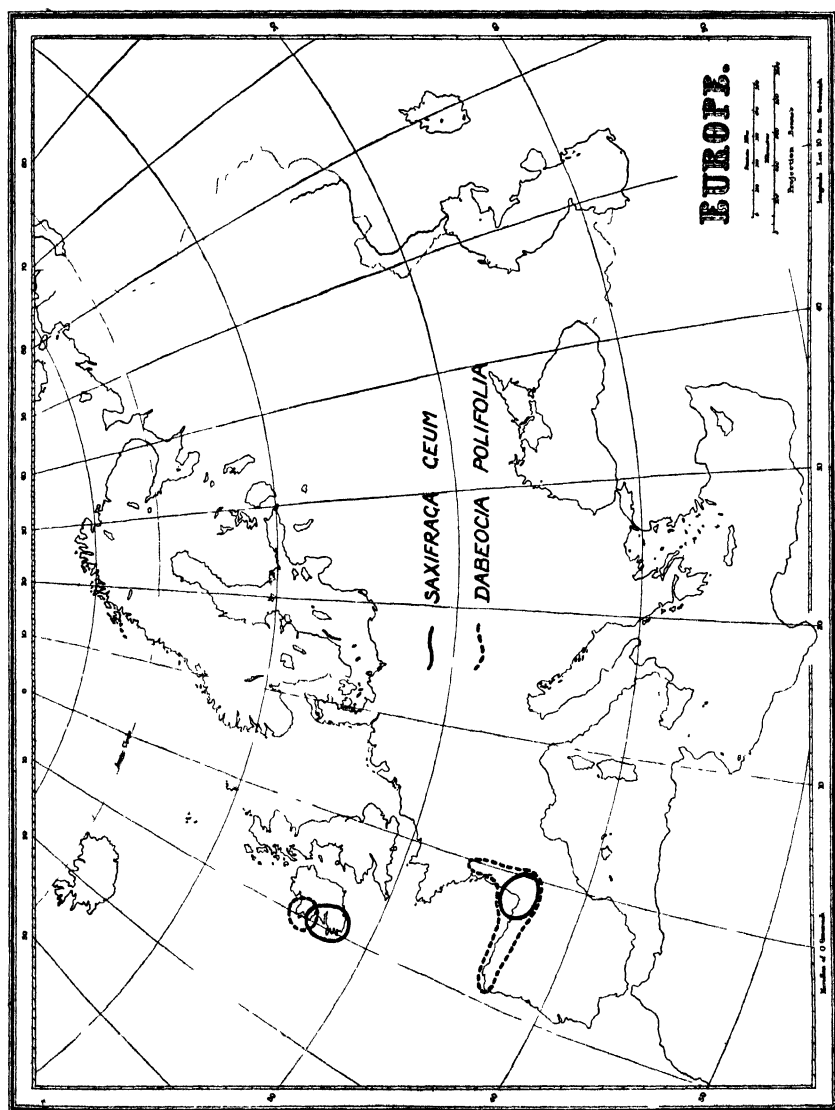


FIG. 56.—Map showing the distribution of *Saxifraga Geum* and *Daboecia cantabrica* (*Daboecia polifolia*).

have crossed the intervening sea. It is therefore clear that this sea has not proved a significant barrier to dispersal.

Again, there is no reason to assume that the Straits of Dover have ever been wider than they are now, and hence they must always have been an even slighter obstacle to plant migration.

It is at this point that the argument usually becomes confused. Most of the Lusitanian plants are not found notably on the European coast north of Spain, and hence it is generally concluded that they must have travelled in order to reach Ireland direct from one to the other. There is, of course, no real reason to assume that this happened. Although the Lusitanian plants proper do not by definition occur in France, there are species which differ from them only in the fact that they do occur in France, that is, that they show stepping stones between Spain and south-west Britain. *Erica ciliaris* and *Rubia peregrina* are such plants. From this it is perfectly clear that the conditions of western France are very close indeed to those required by the Lusitanian plants. This being so, very slight climatic changes of the measure of those which we know to have taken place since the Pleistocene would almost certainly have permitted the passage of species from Spain to Ireland via western France and England.

In other words, it is not necessary, in order to explain the presence of Lusitanian plants in Ireland and south-west England, to do more than to assume that sometimes since the Pleistocene there have been such minor climatic fluctuations as would enable them to travel along the western shores of France and across the Channel somewhere in its narrower part.

But even this last qualification is not strictly necessary, because the sea gap between Brittany and Cornwall is not very much wider than that of the Irish Sea, and need be regarded as but little more of a barrier.

On these facts and arguments it would seem that the Lusitanian and Atlantic species of the British flora do not present so much of a problem as is generally supposed, but that their presence can be explained by migration along the western shores of Europe during a period when climatic conditions were slightly higher than they are to-day—possibly in the early stages of the post-glacial period. It would follow from this that they are comparatively recent immigrants to the Irish flora and there seems no evidence to the contrary.

Included in Matthews' oceanic northern element are six species found on the west side of Britain which outside our country occur only in North America. These are *Eriocaulon septangulare*, *Juncus Dudleyi*, *J. tenuis*, *Sisyrinchium Bermudiana*, *Spiranthes gemmipara* and *S. Romanzoffiana*, the *Junci* in particular being of rather uncertain status. It would seem that the explanation of the presence of these plants in western Europe involves the difficult question of the distribution of land and sea in the past, and they should be recalled when this subject is dealt with in a later chapter.

The general northern element of the flora has an obvious and rather special interest, because it is the one most likely to have survived the Pleistocene *in-situ*. Indeed, it may be accepted as certain that practically all of it did so, and, this being the case, it may claim to be the oldest and most persistent part of the British flora.

It is obviously impossible in one short chapter to do justice to the many interesting features and problems of the British flora, and the very brief outline which has been given should be amplified by reference to some of the original works cited. It is to be hoped, however, that enough has been said to show how

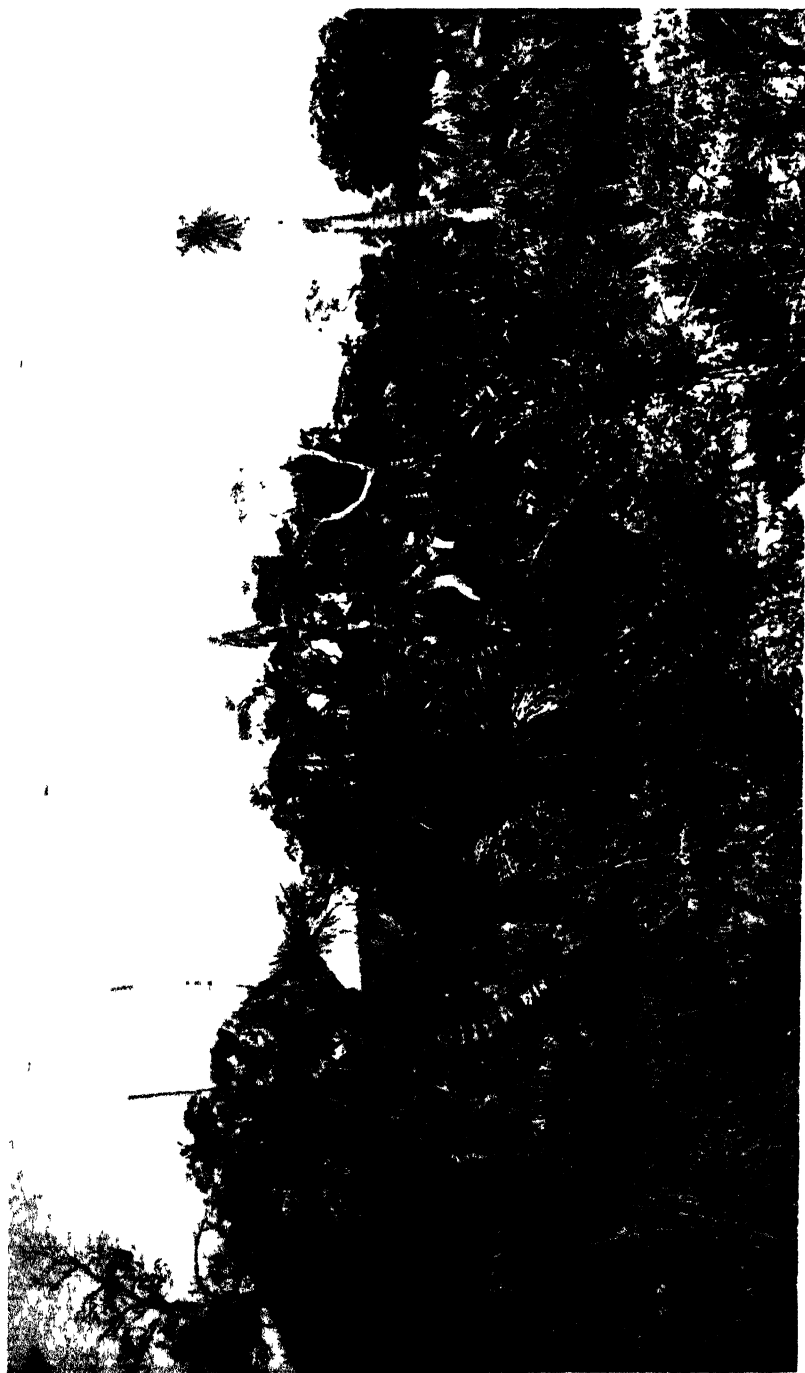


Plate 17. Australian Proteaceae and Arborescent Liliaceae

(from Karsten & Schenck, Vegetationsbilder)

well the flora illustrates many of the fundamental aspects of plant geography, and that it must, for this reason, always be of special significance to the student of plant distribution.

First and foremost it shows in an unusual and perhaps unique way the stages by which a comparatively varied flora has been built up over a long period by immigration following serious and prolonged climatic upheavals. Secondly, it illustrates the extent to which a flora may be influenced and modified by contemporary human history. Thirdly, it epitomises the whole story of the northern temperate regions and their plant life since the Pleistocene. Indeed, it is perhaps no exaggeration to say that the British flora reproduces, in little, much of the whole story of the spread and development of Angiosperm floras, for what has overtaken the British plants in particular has almost certainly affected the whole world flora in more general and less drastic fashion.

CHAPTER 13

THE DISTRIBUTION OF PLANTS IN AN ENGLISH COUNTY

IN the last few chapters the geography of the Flowering Plants has been surveyed with increasing precision by considering first the families, then the genera and the species, and then the distribution of a comparatively small number of species over one particular country—the British Isles. Throughout, however, attention has been directed almost exclusively to the *extent* of distribution, and little has been said so far about the almost equally important subject of the *intensity* of distribution. This chapter is intended to remedy this and to supplement the picture already drawn by describing in comparative terms the distribution of the species in the flora of a yet smaller area, as shown by a recent phytogeographical survey of one of the smaller English counties (282).

The county of Dorset, which was the area selected for study, is small but its topography and geology (fig. 57) are remarkably varied, affording an almost

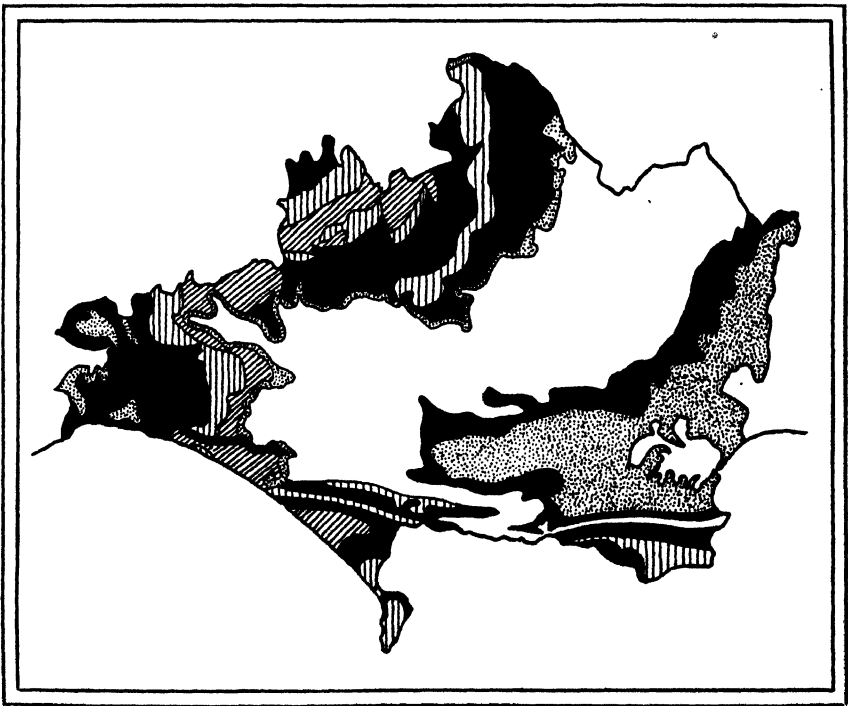


FIG. 57.—Map showing, slightly simplified, the distribution of subsoil types in the county of Dorset :—

dotted—sands,
white—chalk,
black—clays.

vertical shading—limestone,
diagonal shading—mixed clays and limestones.

unrivalled series of plant habitats. In the east, round Poole Harbour, is a low-lying basin of Tertiary sands and clays ; west of this is a wide extent of chalk uplands ; while beyond this again are three distinct series of vales in which the rocks are mainly clays and marls interspersed with various kinds of limestones. Moreover, superficial deposits are very widespread, especially in the centre and west, adding greatly to the complexity of the surface geology. The relief is marked, though there are no heights of more than about 900 feet, and although the county is well watered, its rivers are, except perhaps for the Stour, little more than streams.

The distribution of climatic values in Dorset is still incompletely recorded in detail, but the leading facts are that the rainfall, which has a general average of about 35 inches a year, being broadly correlated with elevation, generally increases towards the west and is least in the low-lying coastal areas ; temperature lines run roughly parallel with the coast, values rising inland in summer and diminishing inland in winter ; sunshine figures are very high, though they also fall inland, and on the whole the county is among the mildest ; south-westerly winds prevail and are frequent and there is little fog.

When the ranges of the different species of its flora are plotted over the county, their chief geographical feature is quickly apparent, namely, that none of them is completely and evenly distributed. Even the commonest plants are absent from some small areas and are of more or less than usual frequency in many others,

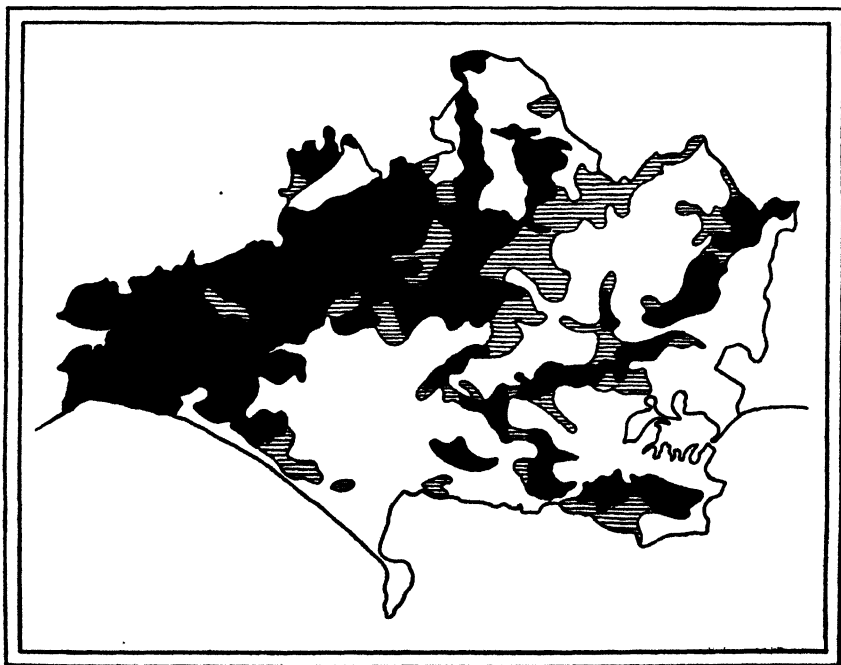


FIG. 58.—Map showing, slightly simplified, the distribution of the primrose (*Primula vulgaris*) in Dorset :—

black—present generally in both woods and hedges.
shaded—present generally in woods but not in hedges.
white—virtually absent from all habitats.

while at the other end of the scale there are certain rare species known only from a single spot and in very small quantity. In short, all show some geographical segregation, and the majority show it to a degree which, in fact, leads them to be absent from at least half the total county area.

It is also apparent that the distributions of individual species vary enormously, both in general character and in detail, and that, although it is true to say that most of them conform to a limited number of main types, it is equally true that no two are entirely alike.

The proportion of the county still bearing relatively natural vegetation is very considerable, and it may therefore be assumed that this general segregation and localisation is not to be attributed primarily to man's actions or to other artificial circumstances, but is the consequence of the natural distribution of factors in the plants' environment, that is to say in the atmosphere and the soil.

In Dorset, as in most similar regions, there is one great difference between the distributions of climatic (atmosphere) and edaphic (soil) values. The former show a continuous range of variation or gradient—they wax or wane gradually in a given direction, but the latter, owing to the disorderly geological pattern, show a patchwork or discontinuous distribution. Moreover, in so far as such things can be compared, the differences among edaphic values are much greater than those of climate, and in consequence, while climate passes gradually from one condition to another, soil character may alter abruptly and completely within a very short distance.

It is, of course, a matter of everyday observation that most plants are found only in certain kinds of habitat, and that their distributions are indeed correlated with edaphic rather than climatic conditions is confirmed by the nature of their individual distributions, which are prevailingly of the second, discontinuous type. This is not to say that climatic factors are, in these cases, to be ignored altogether, and they are undoubtedly often of significance, if only indirectly, by controlling the value of certain edaphic conditions, but a geographical survey of the species within the county makes it clear enough that edaphic factors are paramount in determining not only their ranges but also their relative frequency.

These edaphic conditions will be considered in more detail presently, but first it is desirable to discuss the apparent exceptions to the rule and to note particularly the instances in which a gradient type of distribution indicates that climatic rather than edaphic factors are of significance.

First of all among these there are some forty species whose Dorset records are marginal, that is to say, on the extreme edge, in some direction or another, of their total ranges. A very few of these are northern plants which reach towards the south or south-west only as far as Dorset, as for instance, *Gentiana Pneumonanthe*, but most of them are the opposite, the Dorset records being among their most northerly or north-westerly occurrences. Some of these species are comparatively plentiful in the county, as, for instance, *Erica ciliaris*, though they are always localised, but most of them are rare and sporadic. As far as can be estimated none of them occur in peculiar kinds of habitats such as might be unknown elsewhere in England, and it may therefore be concluded that their appearance in Dorset is, primarily, at any rate, due to the existence there of certain particular and rare climatic values. What these may be cannot be discussed here, but it may be hazarded that temperature is the main component concerned.

A second group comprises a handful of species (among them the primrose, *Primula vulgaris* (283)) which show increasing prevalence of occurrence from east

to west, that is to say towards that part of the county where the rainfall is greater, and the result is that their distributions show so marked a gradient as strongly to suggest that some aspect of rainfall outweighs any correlation they may have with edaphic conditions (fig. 58).

A third or even smaller group comprises species which, within the county, are confined to the more northerly parts of the great chalk belt. The most striking of them is *Filipendula hexapetala*, which extends into the county from the north, with diminishing frequency, as far south-west as Dorchester. *Verbascum nigrum* is interesting, too, because it is almost confined to an area within a few miles of the Wiltshire border. There seems no good reason to suppose that these more northerly parts of the chalk are edaphically very different from the remainder, and it therefore seems clear that the localisation of these plants and their gradient distribution are due to climatic factors of some kind, and presumably that these are related in some way to the proximity of the sea.

One reason for this conclusion is that a considerable number of Dorset plants, forming a large fourth group, have just the opposite kind of distribution, being much more frequent in the vicinity of the coast than elsewhere. It must be made clear that we are not speaking here of those maritime species proper which occur in habitats which feel the direct influence of salt water and which will be mentioned later, but of what may be described as ordinary inland plants generally found fairly well distributed over England as a whole, and it is a remarkable fact that these latter number about a hundred, or roughly one-tenth of the total county flora.

Geographically these plants tend to be of three types: some being confined to a narrow coastal belt; some being chiefly so restricted but occurring sporadically, though less frequently, inland; and some ranging more or less all over the county but with notably greater frequency towards the south. The first include such extreme examples as *Vicia bithynica*, *Trifolium squamosum* and *Carduus tenuiflorus*, which are hardly ever found far from the immediate vicinity of the coast, but most of them are like *Rubia peregrina* and *Linum bienne*, which, though predominantly coastal are not exclusively so. The second type includes *Picris Echioides* (fig. 61), *Echium vulgare* and *Medicago arabica*, which occur not uncommonly far from the sea but which are peculiarly characteristic of the coastal belt. Notable examples of the third type are *Dipsacus fullonum* (*sylvestris*), *Allium vineale*, *Trifolium fragiferum* and *Anthyllis Vulneraria*, but it includes also quite a number of common species such as *Rumex crispus*, *Lotus corniculatus*, *Anagallis arvensis*, *Daucus Carota* and *Galium verum*, all of which increase in frequency towards the coast in a way which cannot be attributed solely to direct edaphic considerations.

It cannot, of course, be argued that the distribution of all these plants is exclusively determined by climatic considerations, but it seems clear that the increasing proximity of the sea is a matter of real importance to them in determining their frequency, and it is difficult to see how this operates unless it does so by modifying the climatic values locally. Only further careful investigation can show how this may come about, but it seems safe to assume that humidity and the presence of salt in the atmosphere have a good deal to do with it. That salt-laden winds from the sea do affect the vegetation inland is familiar enough when unusually strong gales blow inshore in early summer and the young expanding foliage of the hedges and woods becomes killed by the salt in the air. The nearer the coast the more these effects are felt, but they may be noticeable for many miles inland.

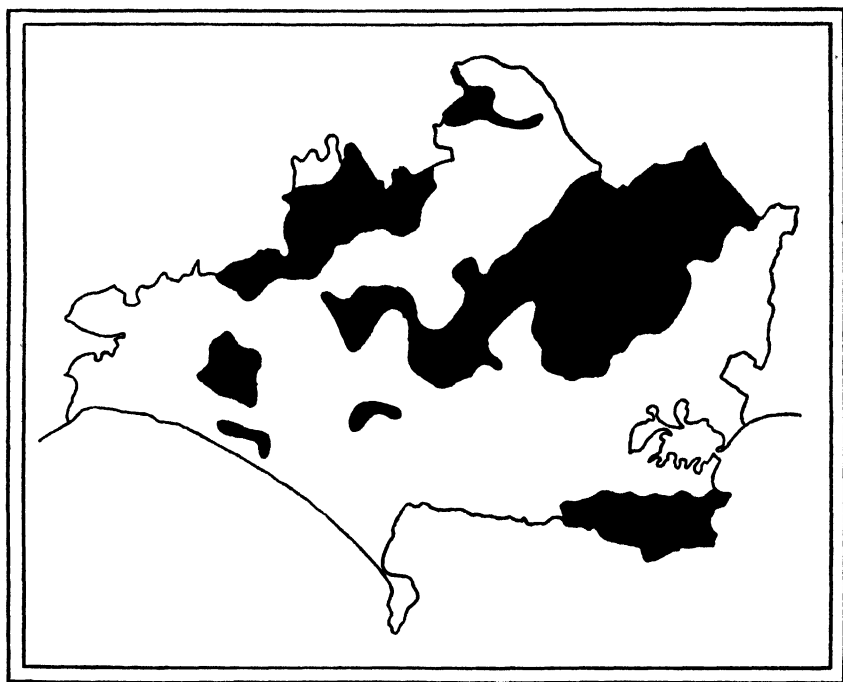


FIG. 59.—Map showing (black) the distribution of *Clematis Vitalba* in Dorset.

To sum up, there is every indication that climatic factors play a considerable, and it may be even an overriding, part in determining the distribution over the county of some proportion of its species, especially if their influences are reinforced by their effects in modifying edaphic conditions locally, but there is no evidence that climate is, in general, more than a subsidiary or secondary geographical determinant.

In the distribution of all the remaining species of the county flora, or at least all those that occur naturally, there is predominantly correlation with edaphic conditions of one sort or another. This is, of course, least obvious in the commonest and most widespread plants, but even here distribution is never quite complete, and the gaps are edaphic gaps, such as is their relative absence from wide areas of the barren sandy soils in the east. Nor do these species elsewhere all inhabit the same range of conditions, each tending to owe its exceptional frequency to particular circumstances, such as ability to flourish in disturbed or less hospitable ground or unusual powers of competition, which express themselves in terms of edaphic correlation. The question of shade and mutual protection is also of great importance, and even the commoner species are usually found either in sunny or shady situations, their comparative abundance being due to their occurrence in almost every variety of one or other of these conditions. A few species, while similar in the main, show also some soil preferences, as, for instance, *Senecio Jacobaea*, *Galium Mollugo* and *Sambucus nigra*.

The less common species, which form the great bulk of the flora, tend to show a more or less rigid restriction to one or other of a small number of major habitat-types, and the general importance of edaphic factors is here particularly clear. Soil conditions vary enormously, but, in the very broadest terms, it may be said that the main variable components are five, all of them related more or less directly to the physiological necessity under which plants live of absorbing water and nutrient salts from the soil, namely the absolute amount of water in the soil; the ability of the soil to retain moisture; the basicity of the soil; the acidity of the soil; and the salinity of the soil. The values of these components depend chiefly on the nature of the parent rocks of the soil, on the topography and on the effects of denudation, and the general effect is to produce six great series of habitats, which may be called, respectively, aquatic, impeded (clay soils), sandy, calcareous, acid and saline. To one or other of these the great majority of species are confined, and only a few show any appreciable ability to occur in more than one, though, naturally, the absolute degree of segregation depends in some measure on the closeness of relationship between the types, it being especially marked between the first two.

Furthermore, most species are less than completely distributed over any one of these. Thus among aquatic plants some, like *Epilobium hirsutum* or *Apium nodiflorum*, are found in almost all watercourses, but others favour certain kinds only such as the more calcareous or silty or acid. Still others, like *Sagittaria sagittifolia* and *Butomus umbellatus*, find conditions to their liking only in the larger and deeper rivers, and others have different preferences again.

Circumstances combine to make heavier and less well-drained soils particularly plentiful in Dorset and there is every kind, from comparatively light loams to the stiffest and most water-logged clays. Some of the species associated with them are therefore very widespread, but most are much more limited. A very important point about this soil type is that it is especially the one on which dense thicket and woodland develops, and its plants therefore include most of the shade-loving species. Indeed plants of these heavier soils may be described as either woodland species or hay-pasture plants.

Of the former a few are fairly widespread, but most are, by the nature of the case, more restricted, as Dorset is not an exceptionally well-wooded county. Among them they illustrate almost every kind of distribution over the woodlands of the area, and the ranges of some of the more local or uncommon, such as *Platanthera chlorantha*, *Melampyrum pratense* and *Ribes rubrum*, are particularly interesting and suggestive. A few species are characteristic of damp bushy places rather than of woodland proper, and presumably find therein conditions particularly suited to them.

The distribution of the meadow plants varies a good deal, because some of them seem equally at home in more than one type of soil, and are thus by way of being exceptions to the general rule. *Chrysanthemum Leucanthemum* and *Primula veris*, for instance, are found in calcareous grassland as well as in clay meadows, while *Deschampsia caespitosa* and *Serratula tinctoria* inhabit clays and certain other soils with a greater tendency to acidity. Of the plants more definitely confined to clay subsoils, *Silaum Silaus* (*S. pratensis*), *Senecio erucifolius*, *Sison Amomum* and *Hordeum nodosum* form a series peculiarly associated with the more calcareous clays. *Picris Echioides* and *Tussilago Farfara* are frequently found on bare clay surfaces, and this may be partly the reason why they are conspicuously more frequent in the coastal zone.

The chief feature of sandy soils is the rapidity with which water passes through them, in consequence of which they easily become leached of mineral salts, and unless there is an impervious layer below them they are often very dry. On such soils two kinds of vegetation, dry heath and dry turf, generally develop, and each has its own particular plants. The former often covers wide areas and *Calluna vulgaris*, *Erica cinerea* and *Potentilla erecta* are prominent in its flora; the latter occurs more locally and its species are less familiar. Still other species are found in sandy places which are damp at certain times of the year.

When the normal drainage of water from sandy soils is impeded and they become water-logged, the soil water is usually acid because of the absence of neutralising bases, and when this condition is extreme a very specialised kind of habitat results which supports only a few particular species, but when, as in Dorset, there are considerable stretches of wet sand and gravel, almost all degrees of acidity are represented and there is a marked zonation in the distribution of species. In the less acid places several species of *Juncus* are prominent; in soils of medium acidity *Hydrocotyle vulgaris* and *Scutellaria minor* are among the characteristic species; while *Molinia caerulea* (fig. 60), *Myrica Gale*, *Narthecium ossifragum*, *Pinguicula lusitanica* and the species of *Drosera* typify habitats of higher acid values.

The calcareous soils of Dorset comprise the chalk and a series of limestones and marls of varied calcium content, and in total cover a considerable part of the county, but the calcicolous species are by no means evenly distributed over them.



FIG. 60.—Map showing (black) the distribution of *Molinia caerulea* in Dorset.

The great majority of these are found not only on the chalk but also on some or most of the other formations (fig. 59); but certain species are much more restricted. *Asperula cynanchica*, *Campanula glomerata* and *Gentiana Amarella* are among those found almost exclusively on the chalk, while *Cephalanthera Damas-onium* (*grandiflora*), *Monotropa Hypopithys* and a few more are confined to it. On the other hand, one or two species occur virtually only on certain limestones other than the chalk.

Although so many species are found only on one or other of these main soil types, there are a few which inhabit a considerably wider range of conditions, occurring not only on clays but in mildly basic as well as in mildly acidic soils. Presumably these plants find in all these soils some common factor of importance, but it is also well to bear in mind the possibility that the apparent wideness of distribution may be due to the fact that the species concerned is complex, with more than one ecotype.

The distribution of the halophytes is superficially rather different from the general scheme because of the naturally localised area of their habitats, but the same kind of edaphic segregation and zonation exists here also. This is specially noticeable in plants of tidal soil water such as occur widely in Poole Harbour and in the neighbourhood of Weymouth, but the more specialised habitats, like sand-dunes and shingle beaches, also have their characteristic species.

Only a few species do not fall easily into one or other of the edaphic classes just described, and therefore appear at first sight to be anomalous, but it seems clear that most of them are not really so but are unusual expressions of one or other of these types, their ranges being determined however by factors which, though similar, are peculiar and therefore less obvious.

Species which occur only in habitats which are the result of man's activities, such as cultivated ground and walls, conform to the same general scheme of things. Since not only the habitats themselves but also their distributions are artificial, the ranges of the species inhabiting them are in most cases rather different from the normal, but this does not indicate any essential difference of plan, and examination shows that there is here just the same kind of segregation according to edaphic conditions and values.

So far we have been speaking chiefly about the extent to which the various Dorset plants occupy the county, but, as was pointed out at the beginning of the chapter, this is only part of the story, and we must consider also the question of the absolute frequency of the species' individuals. There are clearly four main possibilities. The area may be large and the occupation intense, the individuals being both widespread and plentiful; the area may be large and the occupation slight; the area may be small but the occupation intense; or the area may be small and the occupation slight.

Such a fourfold classification is implicit in the usual procedure of describing species as "common," "frequent," "local," or "occasional." It will be noted that the word rare is avoided, since it may refer either to area or numbers, and, indeed, the so-called rarities are plants either very restricted in range or which occur extremely sparingly, and to these the terms local and occasional are best applied.

The commonest species are naturally those which occur in great numbers over a very wide area, and these have already been alluded to, but the more plentiful species in nearly all the main ecological categories may also be called common, and enough reference to these has also been made.

The term frequent is not quite so easily defined, because this condition may result from one or other of what appear to be two different circumstances, namely the frequency with which particular kinds of habitat occur and the degree to which individuals may be discontinuously distributed over the range of one kind of habitat. Actually both these express the same fact, that the plants concerned are restricted to certain particular conditions, though in the one case this is more obvious than in the other.

Many Dorset plants are frequent in the first sense, as for instance many aquatics which naturally tend to occur only here and there, but the second kind of frequency is on the whole the more interesting. Quite a number of woodland plants are far from general in that type of vegetation, and it is notable how much richer in less common plants some woods are than others. *Epipactis latifolia* and one or two other orchids illustrate this among woods on the chalk, while *Chrysosplenium oppositifolium* and *Ribes rubrum* are characteristic of a particular kind of damp woodland elsewhere. Then there are *Orchis Fuchsii* and *Orchis ericetorum* (*elodes*), which not uncommonly grow together but which have quite different total distributions in which the former is much more frequent. Again, many plants of calcareous grassland, such as *Hippocrepis comosa* and *Helianthemum nummularium* (*vulgare*) occur in only some of the apparently favourable places. In all these it is clear that the plants are confined to localities in which special conditions prevail.

Two other species deserve mention in this connection. *Linaria vulgaris* is generally a hedgerow plant, but grows only where it is well exposed and free from shading. It occurs over a wide area mostly on the chalk, and is often enough to be seen, but its occurrences are generally well spaced and it rarely grows in great quantity. *Hypericum Androsaemum* is an extreme instance of the same thing. Its distribution, at least in the west of the county, takes the form of numerous but very isolated records in hedges, where the plant is seldom seen as more than a solitary individual, a state of affairs noted for other parts of England also.

The term frequent is peculiarly applicable also to many plants of unnatural status and habitat. Many cornfield weeds, such as *Specularia perfoliata*, *Agrostemma* (*Lychnis*) *Githago* and *Lycopsis arvensis*, are so, partly because their habitats are discontinuous and partly because each favours particular soil conditions. Similarly with the comparatively few species which normally grow almost exclusively on walls. These by no means occur on all walls but only where special circumstances pertain.

Just as many fresh-water aquatics are necessarily frequent, so the halophytic or maritime species proper are of necessity local in the sense that they are confined to the coast, but even here many have quite a narrow range. Among the salt-marsh species, for instance, *Althaea officinalis* is found only in the Fleet west of Weymouth; and among cliff plants *Brassica oleracea* is virtually confined to Purbeck.

Of inland plants all those which live in highly specialised habitats tend to be local because their situations are so, but this is only to be expected, and it is certain other species which are the most interesting of the locals.

Outstanding among them are the two great treasures of the county flora, *Erica ciliaris* and *Pulmonaria longifolia*. The former is confined to a small part of the southern heathlands, and nearly all its records are from an area of about fifteen square miles, although here it is plentiful. The latter is a plant of certain woods towards the east of the county and also ranges mainly over only a few square miles, but here it is relatively much less plentiful. *Wahlenbergia hederacea*

is, elsewhere on the heathlands, almost as restricted, and even more so is *Ophrys sphegodes*, which is limited to a small part of Purbeck.

Viola palustris combines both the local and occasional types. In the west of the county it occurs locally in connection with the Greensand, but otherwise it is occasional only near the Hampshire border in the extreme east.

The occasional species of Dorset naturally include all the great rarities. The extreme is seen in *Himantoglossum hircinum*, which has been known in the county for several years only from a single plant in the Weymouth neighbourhood. Several others have only one locality but therein are in larger numbers. *Melittis Melisso-phyllum* has but one station, where there are two or three plants; *Cyperus longus* has two or three stations and is fairly plentiful in them, and the same is true of *Cladium Mariscus*.

Most of the occasional species are, however, more plentiful than this and, like the members of other groups, can be classified according to the soils in which they occur. The following are interesting examples. Among shade plants *Platanthera chlorantha* is found in many woods and is widely scattered, but is always few in numbers. *Sedum Telephium* has fewer stations but is rather more plentiful in each, and *Corydalis claviculata* is somewhat similar, though rather local in addition. *Calamintha ascendens* and *Nepeta Cataria* occur very occasionally in hedges on the chalk. The rare orchids of chalk pastures, such as *Orchis ustulata* and *Herminium Monorchis*, are also noteworthy, and on sandy soils there are other species, including *Moenchia erecta*, *Pulicaria vulgaris* and *Potentilla argentea*. There are still others among the aquatics, while among the plants of strongly acid soils *Hammarbya (Malaxis) paludosa* is outstanding.

In addition to all these, which except for the cornfield weeds or colonists may be considered native plants, there is a very interesting group of species which seem to have been introduced at some time or other and which vary greatly in abundance and range.

Some are found only near human habitations, though the significance of this is not always clear. *Malva sylvestris* is generally found in hedges near villages and is seldom a constituent of more natural plant associations. Rarer and more conspicuous examples of the same kind are *Chelidonium majus*, *Aegopodium Podagraria* and *Smyrnum Olusatrum*, the last very much favouring the coast region. *Ribes Uva-crispa (Grossularia)* is apparently wild often enough, but there is little doubt that this is due to bird-dispersal from gardens. The same is presumably true of the crab-apple of hedgerows, which is usually simply a wildling which has grown from the seed of a cultivated variety. The true wild crab does, however, also occur rarely.

More obvious denizens derived from shrubbery or garden plants are *Chrysanthemum Parthenium*, *Vinca minor* and *Mimulus guttatus*, while *Linum usitatissimum* and *Onobrychis* are obvious relics of cultivation. *Sambucus Ebulus*, sometimes seen in hedges, and *Inula Helenium*, mostly found in orchards in the northern part of the county, are of similar but more remote origin. *Atropa Bella-donna*, too, is of rather special interest. It is plentiful and frequent in one large private park and occurs occasionally in other parts of the same estate, but there is little doubt that it is an introduction.

Particular problems are presented by a group of Monocotyledons which occur rarely in more or less natural surroundings and among natural vegetation, but whose native status is at least open to grave suspicion. They are *Narcissus biflorus*, *Leucojum vernum*, *Ornithogalum umbellatum*, *Fritillaria Meleagris*,

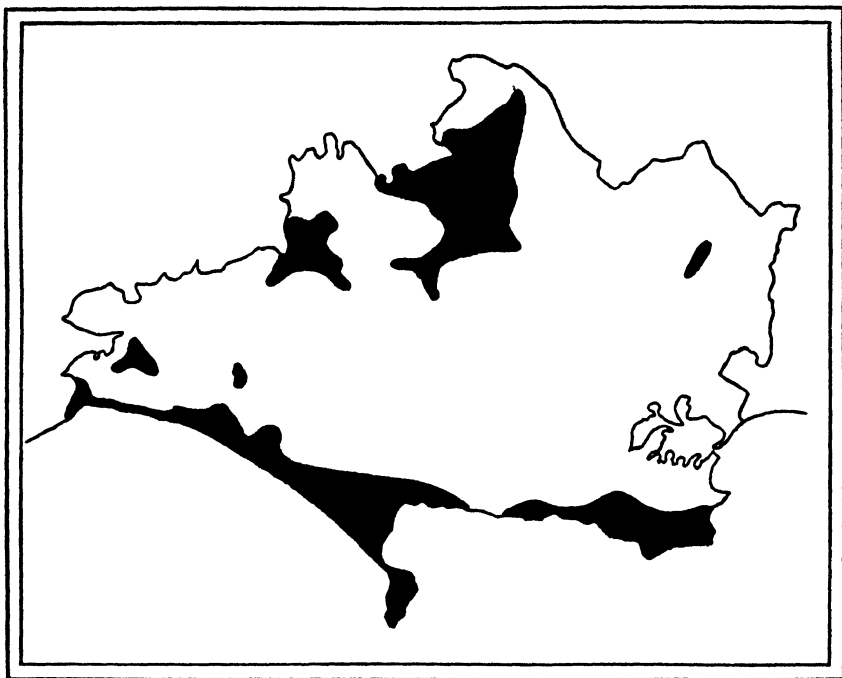


FIG. 61.—Map showing (black) the distribution of *Picris Echioides* in Dorset.

Simethis planifolia, *Acorus Calamus*, *Tulipa sylvestris*, *Galanthus nivalis* and *Convallaria majalis*. All but the last three are almost certainly long-established denizens, and of these three the first has no good claim to recognition as a native.

This chapter may well close with an attempt to estimate the changes which have taken place in the constitution of the county flora in the 150 years or so since systematic records were first collected, because this will help to illustrate several other points of significance and interest in the distribution of Dorset plants.

The continued floristic study of any area tends inevitably towards an increase in the numbers of plants known therefrom, partly because more and more small species are recorded and partly because it is difficult to say what species become, in course of time, lost, and for these reasons there is little doubt that the Dorset flora is, in one sense, richer now than it has ever been. This is probably a fair picture of the balance of change, because it seems certain that additions have more than made up for losses. It is true that the former are mostly denizens or casuals and the latter are mostly native plants, but the general effect is certainly a net gain.

It is, of course, always difficult to be sure that any species has actually disappeared, but there are some which at least have not been seen for many years, and they may be regarded as lost. The most striking examples are *Parnassia palustris*, *Pinguicula vulgaris*, *Empetrum nigrum* and *Hottonia palustris*, all of which have been repeatedly sought for in recent years without result. The most remarkable fact about them is that three of them are markedly, and the last less conspicuously, northern species such as might be expected to disappear in the course

of a gradual climatic amelioration, and that they are plants of this kind is highly suggestive.

On the other hand, the frequency with which certain plants continue to maintain themselves in the same stations is very notable. The first serious collection of county records dates from the end of the eighteenth century, and perhaps the majority of these early records can still be verified, showing that the plants concerned have persisted in the same place for at least 150 years.

Of change in relative abundance there is not much evidence except that some of the rarer plants have become even more uncommon, partly because they have been over-collected and partly because certain types of habitat are now much less frequent. For instance, many of the species of bogs and marshes have diminished with the passage of time owing to drainage, and for different reasons the same is doubtless true of some of the cornfield weeds.

Parentucellia (Bartsia) viscosa is perhaps the best example of a presumed native which is undoubtedly extending its range. Unknown in the county until fifty years ago it has now been recorded from a number of stations. Among adventives the most noteworthy is perhaps *Matricaria matricarioides (discoidea)*. The first record of it seems to have been about the close of last century, but now the plant is abundant throughout the county. Several horticultural denizens are also gradually establishing themselves, among them the lilac (*Syringa vulgaris*), and Montbretia. The former is perhaps bird-dispersed into hedges and the latter is usually a garden outcast.

Finally, the innumerable miscellaneous problems of plant geography presented by even a county flora may be illustrated by reference to one which concerns two cornfield weeds. *Adonis annua* and *Centaurea Cyanus* are both now very scarce in the county, and there is virtually only one persistent station for each. In both cases this is a single arable field and here the plants appear, in the case of the latter regularly, often in quantity. Nevertheless this species never seems to spread from the one field, and the former is generally to be found in only one part of a single field, where it has been known, on good authority, for at least forty years.

It is to be hoped that enough has been said in this chapter to fulfil its purpose, which has been to show that the comparative and relative distributions of plants within the same area is an important aspect of plant geography, and in particular that two general statements are true.

The first is that while climatic conditions may usually be regarded as primarily controlling the area which a species may occupy as a whole, the relative distribution of individuals within this area is, as usually, controlled chiefly by edaphic factors.

The second is that a flora is dynamic rather than static, that is to say, that it is constantly undergoing some degree of change. Some species disappear, and others take their places; some become more plentiful, while others diminish. There are, in short, clearly to be seen indications of changes which, persisting over long periods, may eventually lead to marked and considerable floristic alteration.

THE GEOLOGICAL HISTORY AND PAST DISTRIBUTION OF THE FLOWERING PLANTS

THE attention which was paid, in Chapter 3, to the evolutionary background to the study of plant geography makes it abundantly clear that few indeed of the problems presented by the distribution of plants to-day can fully be understood or appreciated without some knowledge of conditions and events, either actually within or in relation to the plant world, in the past. This being so, the second part of this book, which treats more particularly of the theoretical aspects of plant geography, cannot be appreciated without some preliminary outline of the history of the Flowering Plants and of the circumstances which have led gradually to the state of affairs which has been described in the preceding pages. This chapter is therefore devoted to a short account of their history and of their distribution in the past.

The Geological Time Scale

In the course of secular time the vegetation of the earth has gradually changed and developed by the processes of evolution. Little is known about the earliest plants of all, because they have left practically no traces behind them, but they were certainly gradually supplanted by new types. These newer types in turn gave way to others, each new development giving, for the time being, a particular character to the world vegetation.

This knowledge has come from the study of what is often called the "record of the rocks," that is to say, of the organic remains which, from time to time, have become imprisoned in sedimentary deposits, where they are familiar to us in the form of fossils. The story of fossil plants has been most graphically and admirably told by Seward in *Plant Life through the Ages* (215), and this, or the much shorter account of Reid and Chandler (199), should be consulted by those readers who wish to amplify the outline contained in this chapter.

It is believed that plant life began in the sea, and that plant evolution has been largely directed towards the attainment of the complicated and beautiful structural organisation which enables modern plants to colonise the land surfaces of the earth, and to exist as successfully in a subaerial medium as they did formerly and still do, to some extent, in subaqueous and particularly marine habitats. That is to say, it is, in a single phrase, the change from the kind of form possessed by such plants as the seaweeds to that exhibited to-day by the Flowering Plants. Coincident with these structural developments there have been equally great changes in reproduction and in life history.

The fossil record indicates that the history of each new group of plants has always followed much the same course. First, there appear a few isolated examples of the new type. Then gradually, but at a constantly accelerating speed, these new types multiply until in a comparatively short time they become the dominant vegetation of the world. This position of supremacy they hold for a

while, and then, as rapidly as they rose, they tend to diminish before the competition of still newer plants until eventually they disappear entirely or persist merely as a few meagre survivors of a great but long-dead past. Not all newly evolved plants necessarily pass through the whole of this cycle. Many never succeed in establishing themselves; others may do so on a small scale but never develop into important elements in the vegetation. Nor must we think of this developmental cycle as something peculiar to plants. It is found in all aspects of life and even in the life of the individual. He is born; he slowly or more rapidly reaches maturity; he flourishes or the reverse; and he more slowly or rapidly declines, until he finally and inevitably passes away.

The whole sequence of rocks that have been formed since the beginning of secular time is divided by geologists into five great eras based chiefly upon the kinds of fossils that the various formations contain. The first era consists of the oldest rocks, and these include no fossils, because they represent a time when life on the earth, if it existed at all, was of so simple a kind as to have left no traces. This is called the *Archaeozoic* era. Next comes the *Proterozoic* era, the rocks of which contain some evidence of life, but only of the most primitive sort. This is followed by the *Palaeozoic* era, and here, for the first time, the plant remains become abundant and unmistakable, though they all represent ancient groups of plants such as ferns, club mosses and the very earliest and simplest kinds of seed-plants. Next comes the *Mesozoic* era, during which the vegetation consisted chiefly of ferns and *Gymnosperms*. Finally, there is the *Caenozoic* era, and this is generally described as the era of the Flowering Plants.

Each of these eras is divided into shorter time divisions called periods. Of the *Archaeozoic* and *Proterozoic* eras no mention need be made here since they are so far in the distant past as to be outside our immediate consideration. The *Palaeozoic* era is divided into six periods called respectively, and beginning with the oldest, *Cambrian*, *Ordovician*, *Silurian*, *Devonian*, *Carboniferous* and *Permian*. The *Mesozoic* era consists of three periods, *Triassic*, *Jurassic* and *Cretaceous*, and the *Caenozoic* era of several periods, divided into *Tertiary* and *Quaternary*. To-day we are living in the last named.

This short description of the geological eras and periods almost inevitably leads to the question of the length of geological time. Many answers have been given to this question but none can claim to be more than an estimate. That the total is to be reckoned in millions of years cannot be doubted, but how many millions it is impossible to say. Much depends on the method of estimation used, and readers may be referred to Holmes (125) for an account of these. It can only be said here that estimates range from something of the order of 20 millions to something exceeding 2,000 millions, but probably a space of some hundreds of millions is nearer the mark.

As to the proportion of the whole occupied by the different eras, it is generally agreed that the *Archaeozoic* and *Proterozoic* together account for more than half geological time; that the *Palaeozoic* accounts for nearly one-third; and that only about one-sixth is occupied by the *Mesozoic* and *Caenozoic* eras. Figures actually quoted by Knowlton (142) are 55 per cent., 30 per cent., 11 per cent. and 4 per cent. respectively, and these agree well with the average ratios of a number of other authors quoted by Holmes.

But millions and percentages convey little, and it is worth while to put the matter in more picturesque form. This can be done by imagining the whole of geological time to be represented by a vertical stick 36 inches long. On this stick the first

two eras will occupy the bottom 20 inches or so ; the Palaeozoic will cover the next 12 inches ; the Mesozoic, 4 inches ; and the Caenozoic, about $1\frac{1}{2}$ inches. Of this last era the Tertiary will account for all but about one-twentieth of an inch. At this end of the scale the time divisions are more comprehensible and another illuminating statement can be made. If, working backwards from the present, the generous estimate of 10,000 years is allowed for the duration of human history proper, then this time, the time during which man has ruled the world, will on the scale be represented by something of the order of one-thousandth of an inch, that is to say, less than the thickness of the thinnest tissue paper. Fig. 62 is a pictorial representation of the upper half of the geological time scale and shows most of the figures and divisions which have been mentioned.

The Caenozoic era was described as the era of the Flowering Plants, and an account of the history of these plants will therefore chiefly concern this time. This is not altogether so, however, because the Angiosperms certainly made their appearance some time during the preceding Mesozoic era, although it was not until the Caenozoic that they became abundant.

As was stated above, the Mesozoic era is divided into three periods, Triassic, Jurassic and Cretaceous, and the first of these contains no fossils for which an Angiosperm nature can be claimed. In the Jurassic, on the other hand, there are several fossil types which, it has been submitted, represent very early and primitive kinds of flowering plants. Chief among these is a group of plants called the Caytoniales, described from the Jurassic rocks of the Yorkshire coast. They need not be discussed further here, but those who wish to know more about them may refer to the writings of their discoverer, Hamshaw Thomas (244), and to the more recent comment of Walton (293). It should also be mentioned that some of the Jurassic Cycadophyta are also thought to be the immediate ancestors of at least certain of the Flowering Plants.

The first undoubted fossil Angiosperms are recorded from rocks of the Cretaceous period. For the most part they represent the remains of leaves only, but they include a few fruits, notably those of a plane tree, and they are in general indistinguishable from modern types of Angiosperms.

This point brings us to one of the most curious features in the fossil history of the Flowering Plants, which is that the group appears almost suddenly and, as it were, ready made. There is scarcely a trace at all of any introductory types. In one series of rocks the plants are entirely absent ; in the next they are present, not only in considerable numbers but apparently also in many of the forms they include to-day. This sudden rise of the Angiosperms has long been an unsolved problem, and Darwin, indeed, refers to it as "an abominable mystery."

One possible explanation is that a notable gap exists in the fossil record just at the time when the Angiosperms were beginning to evolve, so that no traces remain of their earliest forms. It must not be assumed that the whole of geological time is represented by sedimentary deposits. Very probably long periods of time elapsed during which conditions were unsuitable for the formation, or at least persistence, of rocks of this kind, and it may be that the Flowering Plants actually originated during what is now a gap of this kind. On the other hand, fossils of the earliest Angiosperms may exist in some remote part of the world where they have not yet been discovered. Whatever the truth may be, however, their early history is at present largely wrapped in mystery. All that can be said with safety is that they were well established by the latter part of the Cretaceous period and had by then become a conspicuous element in all fossil floras. By the

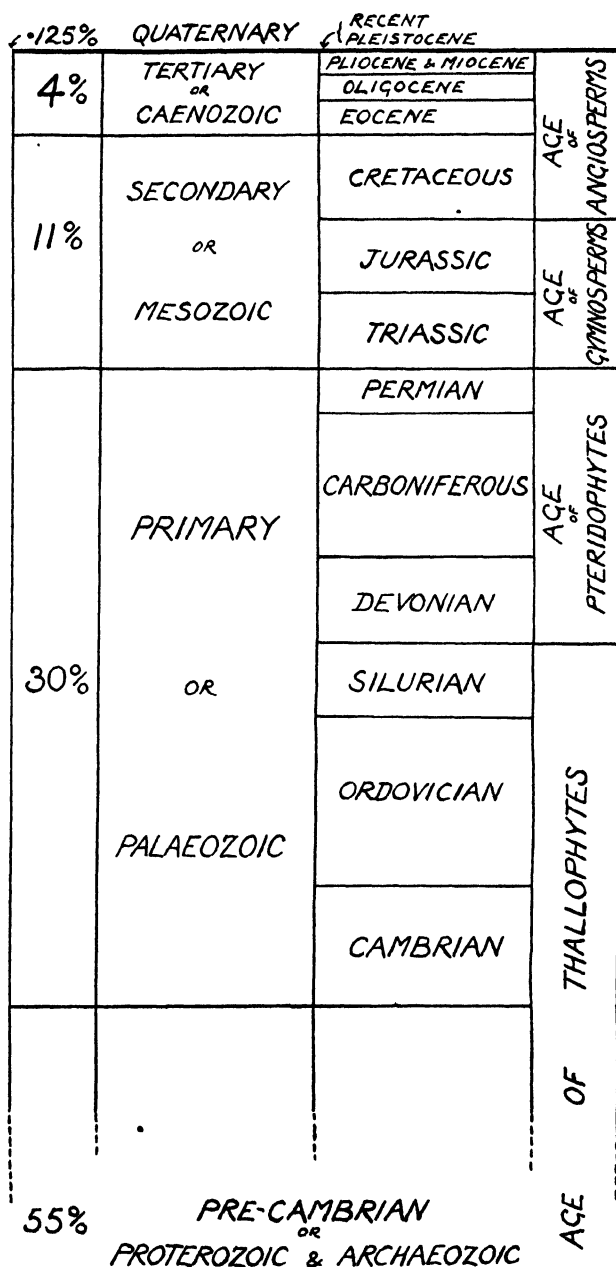


FIG. 62.—Diagrammatic representation of the upper half of the geological time scale.

The figures are percentages of the whole of geological time. The Quaternary is entirely comprised within the slightly thicker top line of the diagram. Compiled from various sources.

beginning of the succeeding Caenozoic era they had become the dominant plants of the world, a position they have retained ever since.

The Caenozoic era is divided into two, the Tertiary and the Quaternary, but this division is in many ways an artificial one, and from the botanical point of view there is little reason for it, because the same types of plants persisted through both. At the same time the division does mark and emphasise a very important stage in their history.

The Tertiary is again divided into four periods, named the Eocene, the Oligocene, the Miocene and the Pliocene, the first being much the longest. Throughout at least the first three of these the general conditions of climate in the world seem to have been fairly constant, and tropical or warm-temperate conditions seem to have been widespread, as indeed they also appear to have been during the later part of the Cretaceous. There was some change, it is true, in the main towards a lessening of temperature values, but these changes were comparatively small. By the beginning of the Pliocene, however, evidence of change increases, and in the course of this epoch the change became accelerated and almost catastrophic. For reasons which are complex and scarcely fully understood, the temperature, at any rate in higher latitudes, deteriorated very rapidly and finally sank to levels that resulted in widespread glaciation. For the first time for millions of years, conditions of ice and snow returned to the earth and there arose the kind of steep temperature gradient between the equator and the poles which is familiar to-day. It is this relatively sudden change of climate that is made the basis of the artificial division of the Caenozoic era into two parts, the Tertiary being considered to end with the oncoming of glaciation and to pass into the Quaternary, which comprises the whole of subsequent history. The Quaternary is itself divided into two, the Pleistocene period, which comprises the actual glacial ages, and the Recent period, which comprises the time which has elapsed since the latest glaciation, but this is an even more artificial separation, because this latter time is very short and affords no real evidence that the glacial ages have in truth ended, so that it may rather be but an interval between two of their more extreme manifestations.

The Identification of Fossil Plants

It was explained at the beginning of this chapter that our knowledge of plants in past ages is derived entirely from the fossils which are to be found in the various sedimentary rocks. At first sight this might seem a very simple and satisfactory source of information, and this indeed it would be were it not that the accurate identification of plant fossils, and especially those of flowering plants, is, for reasons which must be considered shortly here, a matter of great difficulty.

This difficulty arises from two distinct but related circumstances. The first is that the process of preservation in the rocks, or fossilisation as it may be called, is hardly ever so satisfactory as to reveal more than a small proportion of the characters of the plants involved. The second is that plant fossils rarely consist of more than a few small detached organs. Never is there found a fossil which comprises the complete whole body of any plant of appreciable size.

The actual methods by which fossils are found are such as also to add to the problem. This is not the place to describe these methods in detail—fuller information about them must be sought in standard works on palaeobotany—and it is enough here to point out that by far the commonest and most abundant plant



Plate 18. Liriodendron Tulipifera

*(from The Standard Cyclopaedia of Horticulture by L. H. Bailey,
by permission of The Macmillan Company, New York)*

fossils are of the sort called "impressions." These, as their name implies, are in fact prints of the original tissues left from the pressure of their outline and relief on the texture of the sediment in which they became imbedded. These impressions are comparable with the "rubblings" by which such low reliefs as the designs of old brasses and old coins are reproduced, and they bear much the same kind of relation to the original. In short, they reproduce the outline and, to some extent, the surface relief of the tissues but do little else.

By certain other methods of preservation, such for instance as petrification, where the whole tissue becomes impregnated with silica, much more is revealed, and where portions of flowers, fruits or seeds are concerned even impressions are generally enough to allow of fairly trustworthy identifications, but where leaves only are involved the difficulty of accurate determination is very great. Unfortunately, as has been said, the great majority of Angiosperm fossils at least are the impressions of leaves only, and the problems involved in identifying these colour the whole picture of the fossil record of this great group of plants.

Let it be said at once that the plant geographer has always been and is likely to remain under a deep obligation to the palaeobotanist, and it would indeed be ungrateful to belittle this debt in any way. At the same time palaeobotanists themselves would certainly be the last to wish that this sentiment should hamper a critical discussion of the difficulties attending the identification of Angiosperm fossils.

This problem of identification can best be expressed in the form of two questions. How far can leaf form be accepted as diagnostic of different kinds of flowering plants? How far can the characters and form of a whole large plant be deduced from the features of a few detached leaves?

As regards the first question it can only be pointed out that leaves are the most plastic and variable of all plant organs, and that the number of types and designs of leaves is infinitely smaller than the total number of plant species, so that there are many plants with almost identical leaf forms and designs. In some cases, of course, the foliage of a single plant species is characteristic, as, for instance, we assume to be the case in the tulip tree (*Liriodendron*) (Plate 18, fig. 63), which has leaves unlike those of any other known tree; but even this is not quite enough,

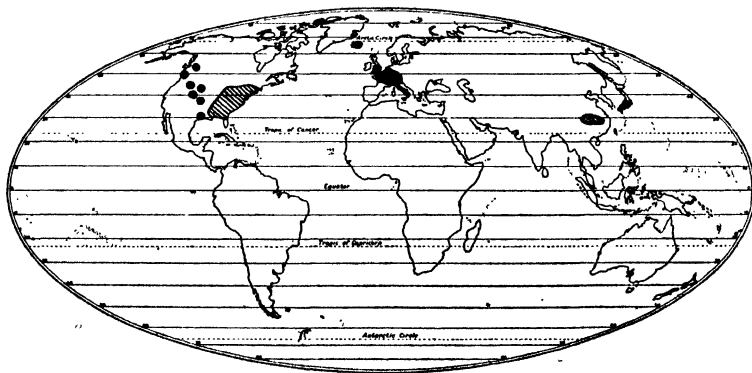


FIG. 63.—Map showing the past (black) and present (shaded) distribution of the genus *Liriodendron*, partly after Berry.

because it does not establish beyond doubt that this is equally true of the past and that every fossil leaf of this pattern belonged to this genus. Indeed, to suppose that all fossil leaves can be identified with plants which are alive to-day is demonstrably fallacious, since there are certain fossil leaves which bear no resemblance to those of any known living plant. These clearly cannot be identified with any modern plant, and it may well be that some other fossil leaves which superficially resemble those of known plants actually belonged to different ones.

But the case of *Liriodendron* is quite exceptionally straightforward, and the great bulk of fossil leaves are of far more generalised types, such as are possessed to-day by numbers of distinct and unrelated plants, and in these cases identification is often difficult and sometimes well-nigh impossible.

The second question also admits of no ready answer. It is only necessary to pick and compare a number of leaves from different parts of the same plant to realise how difficult it is to say that any one is specially typical and characteristic of the species to which the plant belongs. There is nearly always variation among the leaves of any one plant, and more aberrant examples may often resemble the more typical leaves of a species other than that to which they in fact belong.

Furthermore, individual detached leaves do not necessarily reveal all the characteristics of the foliage of the plants to which they belong. Such features as leaf-number and arrangement are generally far from clear, and it is even sometimes difficult to determine whether a fossil is really a complete simple leaf or only a portion of a compound one.

Thus it will be seen that the identification of detached fossil leaves is full of pitfalls, and it is not surprising, therefore, that many attempts have been made to elucidate, by special methods of preservation, characters of the fossils which may not at first sight be readily apparent. For instance, minute details of cuticle structure have often been studied in the hope that they may substantiate determinations, either by their own virtue or in conjunction with other features; but the results have not been altogether satisfactory, since similar types of cuticle structure are frequently possessed by plants of quite different affinities.

In view of these difficulties it is generally admitted that identifications and records based solely on detached fossil leaves, that is to say, on leaves unattached to any axile structures and unaccompanied by other organs, must be regarded with caution and treated to a certain extent as provisional, requiring confirmation or correction as and when means of doing this become available. This is not, of course, to condemn all such records as unreliable. There is little doubt that many of them are correct, but it is only fair to say that these are generally those of least importance and tend simply to confirm what has been discovered from other sources. On the other hand, where fossil records have raised the greatest problems it will usually be found that the records and determinations must themselves be regarded as problematical. The problems may exist, but the evidence that this is so can only be called unsatisfactory.

It is worth while to illustrate this point by one of the most outstanding examples of it, namely, the oft-reported occurrence as fossils in the northern hemisphere of genera and species now more or less rigidly confined to the southern hemisphere and generally considered characteristic of that zone. In particular, many fossils have been ascribed to *Eucalyptus* (now virtually confined to Australia) and to the Proteaceae (almost entirely southern in distribution). If the determinations of these fossils are correct they may completely alter our whole conception of the

origin and development of Angiosperms. Yet when the matter is further investigated and the specimens and illustrations examined, it can be said with perfect fairness that there is no single completely non-controversial fossil among them. In every case the identification is open to some reasonable doubt on purely morphological grounds, and this is the case even in the rare instances where the fossils are the remains of fruits rather than leaves. In short, these fossils may, as some authorities firmly believe, be the remains of the plants mentioned; but they may not be so, and there often seems little *prima facie* reason for their identification. While some authorities accept them others (5, 16) reject them, and they must certainly be regarded with an open mind.

Angiosperm fossil floras vary considerably in content, no doubt according to the actual circumstances of their origin, and fortunately not all consist exclusively of detached leaves. Some contain a few fruit or seed structures among numbers of leaves, and a few consist entirely or largely of reproductive structures. These latter are of special value and importance, not only because reproductive structures are actually more diagnostic than foliar structures but also because they are much less plastic and vary much less as a result of differences in the environments of the plants which bear them.

Apart from the difficulties of identification there is inherent in the fossil record the difficulty, amounting sometimes almost to impossibility, of correlating the geological horizons in different places and of synchronising the floras which they contain. Were it possible to be certain of the correspondence and relationship between strata widely separated in space, the advantages would be twofold. It would be possible to place the floras of the past in their proper chronological order and to see without confusion the succession in which the different types flourished, and, in addition, it would be possible to trace the variation over the world's surface among contemporary floras. At present it is almost impossible often to say which of two fossil floras is the older or whether two floras from distinct regions are of the same age.

It is chiefly because of these difficulties that no one can say exactly when in the course of geological history the Flowering Plants originated. The normal processes of evolution also militate against the recognition of a hard and fast date of first appearance. As far as our immediate purpose is concerned, therefore, it is best to place an arbitrary limit to the enquiry and to begin the story of these plants at the point when they first begin to form an appreciable proportion of the whole existing plant world.

There is unanimous agreement among palaeobotanists that the earliest fossil floras containing a considerable proportion of undoubted Angiosperms belong to the older part of the Cretaceous system, itself the last of the three great periods into which the Mesozoic era is divided. There also can be no doubt that the Angiosperms arose, by the processes of organic evolution, from some pre-existing group of plants, although what kinds of plants these ancestors were is uncertain. It is thus comparatively easy to answer two of the three leading questions relating to the origin of the group, namely, how and when they came into being, but the third question of where this may have taken place is still very debatable. The reason for this resides in another of the limitations of the fossil record, but in this case it is a limitation which may eventually be removed.

It is that naturally enough the fossil plants of those parts of the world, North America and Europe, where scientific investigation has the longest and most important history, are vastly greater in number and much better known than those

of other regions where the opportunities for their study have been fewer. Coupled with this is the fact that the actual land surfaces of the northern hemisphere are much greater than those of the south and may therefore be expected to contain a much larger absolute number of fossils. For these reasons the fossil record is to a great extent the record only of the north. There are, it is true, a considerable number of fossil floras recorded from the tropics and from below the equator, but these are inconsiderable in comparison with those of the north. This is not to say that tropical and southern floras are necessarily of less importance than others, and indeed it is probably to them that we must look for the solution of many problems, but at present at least they are too few and too little known to contribute much to the general story. Such as are known are, however, mentioned in many of the chief works on palaeobotany and can, if desired, be referred to there.

Hence it is true to say that the fossil record is of little assistance in elucidating the place of origin of the Flowering Plants. There are various opinions as to where this may have been, but these are generally based on deductions from the present distribution of plants rather than from the past, and the fossil Flowering Plants known to-day scarcely support any particular hypothesis unless it be that some of them, at any rate, may have originated in what are now the arctic regions.

The answer really largely depends upon another question which at present cannot be answered definitely, namely, whether the Flowering Plants as a whole are to be regarded as having had a monophyletic origin or not. That is to say, whether they are all related by descent from a single common ancestor or small group of ancestors or whether they have originated from a number of relatively distinct ancestral types, their general similarity being due to convergent, or at least parallel, evolution. If the former is true, then they must have had a single place of origin, but if the latter is the case, they may have arisen in a number of different places and even perhaps separately in both northern and southern hemispheres, as well as possibly in the equatorial zone itself.

At present this is still unrevealed. The fossil record alone may in time provide the necessary clues, but it is also to be remembered that progress in many other branches of knowledge, such as, for instance, palaeogeography and palaeoclimatology, may be of great assistance, and it is necessary for the botanist who is interested in this problem to keep abreast of developments along these lines.

The Floras of the Past

The chief Cretaceous fossil floras are found in North America and in Greenland, though others of rather less importance have been described from many other parts of the world, including a number from Europe.

Opinion about the age of the Greenland floras differs. Seward (214, 215) says, "It is probably true to say that in no other part of the world have familiar types of Angiosperms been described in rocks as old as those of Greenland." Knowlton (142), on the other hand, considers them to be of Upper Cretaceous age. These floras are very rich and include such genera as *Artocarpus*, *Platanus*, *Ocotea*, *Cinnamomum* and *Magnolia* (215).

Apart from Greenland, probably the oldest flora containing a considerable number of Angiosperms is the Potomac flora of Maryland and Virginia. There

are also several rich Upper Cretaceous floras in North America, including the Raritan of New Jersey, the Dakota flora, the Tuscaloosa flora of Carolina and Alabama, and various floras in Alaska (123).

Regarding the constitution of Cretaceous floras in general, Berry (15, 17) has emphasised the fact that they contain a mixture of what would be called to-day tropical and temperate genera such as is now found in south Chile, south Japan and New Zealand. That is to say, they may be described as indicating the occurrence in their time of a warm-temperate or subtropical climate.

The question of the extent to which fossil floras are evidences of climatic conditions is a very important one. There is in general no doubt that deductions based on the nature of fossil plant remains are sound, provided of course that the determinations of the fossils can be relied upon. This is particularly well illustrated in some of the earlier descriptions of floras from the arctic regions. Many of the fossils in these were originally attributed to genera of a tropical or subtropical character, and on the strength of this there grew up the belief, still widely held, that during the earlier stages of Angiosperm history the climate was of corresponding value up to the highest latitudes. More careful comparison of these fossils with modern plants, however, seems to show, as Berry (20) has pointed out, that these "tropical" identifications are unsound and that the plants must rightly be attributed to more temperate genera.

Chaney (41) has similarly thrown doubt on the determination of many North American fossils, and in particular records his belief that of the 150 fossil species of *Ficus* described therefrom, the majority belong to other and "less romantic" genera.

It would seem therefore that the opinion formerly held that a tropical or, at least, subtropical climate extended in the Cretaceous and early Tertiary almost or quite to the North Pole must be modified. That there was a well-developed vegetation there is evident enough, but that it was anywhere in these high latitudes of more than temperate facies and relationship is very doubtful. But whatever may be the exact truth about this, the impression left by the Cretaceous floras is that in their time the temperature gradient from the equator to the poles was much less steep than at present and that floras were more widespread and generalised in character.

This state of affairs seems to have persisted into the Tertiary, and the actual passage from the Cretaceous reveals no marked floristic change, so that the distinction between the two is, on this count, rather an arbitrary one.

By the end of the Cretaceous the Flowering Plants had attained that predominance in the plant world that they have ever since maintained, and the fossil floras of the Tertiary, which are innumerable, all show the same general constitution that is to be seen in living floras.

Much the greater part of the whole Tertiary era was occupied by the Eocene, and fossil remains of this time are abundant. The coastal plain of eastern North America (21) has revealed thousands of fossils and seems to have been inhabited successively by three rather distinct floras—the Wilcox flora, the Claiborne flora and the Jackson flora, all of which contain some markedly tropical types. Further west in North America the Raton flora from Colorado and New Mexico was probably contemporary with the Wilcox; the Fort Union flora extended far to the north; and in the coastal region the Puget flora may be of the same age as the Fort Union. Particularly, in thinking of these latter floras it should be remembered that the Rocky Mountains did not then exist, at any rate in anything

like their present form (19). The early Tertiary floras of Alaska are also considerable (124).

In Greenland the Eocene floras are generally thought to date from the latter part of the period. They are especially abundant and well known in the neighbourhood of Disco Island on the west coast, at a latitude of nearly 70° N. They contain many forms which to-day are characteristic of the north-eastern United States.

In Britain there is a small flora, presumably of early Eocene date, from the island of Mull, but far more extensive and important is the great fossil flora of lower Eocene age from the London Clay of what is now the London Basin. Not only is this flora very rich but it consists almost entirely of very well-preserved fruits and seeds and flowers, so that the identifications of its constituents are unusually reliable.

This great flora has been re-studied and monographed on a monumental scale by Reid and Chandler (200). Practically all the specimens are illustrated in a series of fine plates, and the result is a singularly convincing volume whose conclusions permit of little or no difference of opinion. The flora consists of about 250 species, and these include the palms *Nipa* (Plate 19, fig. 64) and *Sabal*, as well as *Cinnamomum*, *Endiandra*, *Hugonia*, *Iodes*, *Leucopogon*, *Litsea*, *Magnolia*, *Meliosma*, *Ochrosia*, *Lanea* (*Odina*), *Olax*, *Oncoba*, *Spondias*, *Symplocos*, *Tetracera*, *Tinospora*, *Toona* and *Vitis*. Although the list of determinations is rather different, the flora is on the whole like the other Eocene floras mentioned, the difference being largely due to the fact that the well-preserved fruits and seeds permit an exceptional accuracy of determination and discrimination.

Reid and Chandler's monograph does not confine itself merely to the description of the fossils but discusses this and other Eocene floras in a most interesting way. The authors reach a number of conclusions of which the most important to note here are that the flora is of the tropical rain-forest type; that it has a marked affinity with the present flora of Indo-Malaya; and that it probably reflects a mean annual temperature of about 70° F.

The impression given by the Eocene floras serves to emphasise that derived from Cretaceous remains. There was no appreciable break between the two

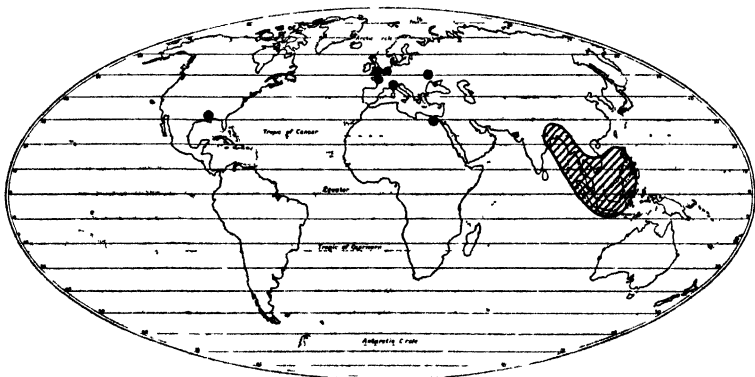


FIG. 64.—Map showing the past (black) and present (shaded) distribution of the genus *Nipa*, after Berry.

periods either in plants or in climate, and the latter was, so far as the vegetation is concerned, apparently an extension of the former. The two together suggest strongly that there may have been something in the nature of a single extensive and generalised flora over much of the whole world or at least over the northern hemisphere.

The Oligocene period which succeeded the Eocene left comparatively few fossils. It is fairly well represented in Europe, including the south of England, and in North America, but there is only one flora that calls for special mention here. This is the Bembridge flora from the Isle of Wight, which like that of the London Clay has been monographed by Reid and Chandler (198). It is not a very large flora, and in general rather resembles the Eocene Wilcox flora except that there are rather more herbs. Its special interest is the resemblance and affinity that many of its plants bear to types at present found only in North America and Asia, and there is an inference, if no more, that these plants may, in Oligocene times, have been part of a completely circumboreal flora, the greater part of which has since been destroyed, leaving only two widely separated remnants.

Although the Oligocene floras are scanty, they are sufficient to show that here again there was little real change accompanying that from the Eocene to the Oligocene. That there is some change is true, but the comparison of the Bembridge flora with the Wilcox is enough to suggest that it was relatively slight.

The Miocene period is, like the Oligocene, short compared with the Eocene and has correspondingly fewer remains, and the important floras of the time are found chiefly in western North America and in Europe. One at least from each region needs special mention.

The first is the Florissant flora from Pacific North America (45), which is actually one of several floras closely related in time and space. It contains about 250 species, among them being many plants familiar in similar latitudes to-day.

The second outstanding flora is that from Oeningen in the neighbourhood of Lake Constance and should perhaps be reckoned as partly Oligocene and partly Miocene. It, again, is but one of a number of floras which together have been described by Knowlton as "probably the richest plant deposits known anywhere in the world." The total number of species described approaches a thousand, but the flora of Oeningen itself contains about 500, some quarter of which are herbs. Most of the fossils are beautifully preserved and enhanced by the fineness of their details. They include, moreover, a good proportion of flowers and fruits.

The identifications of the Oeningen fossils show that the flora was in general very much of the same kind as the Florissant or, at any rate, consisted of plants which are associated with similar conditions of climate. Both, however, differ appreciably from any preceding floras in that they indicate a climate rather, and perhaps much, colder. It would appear, therefore, that during the Miocene the climate and flora, which had been comparatively constant for so long, began slowly to change, and that in the direction of more temperate conditions.

But this is not the only way in which the Miocene indicates change. It was a time of great earth movements and of intense volcanic action and mountain folding, and it is from this period that the greatest mountain ranges of the world date.

The last of the Tertiary periods, the Pliocene, is generally considered to have

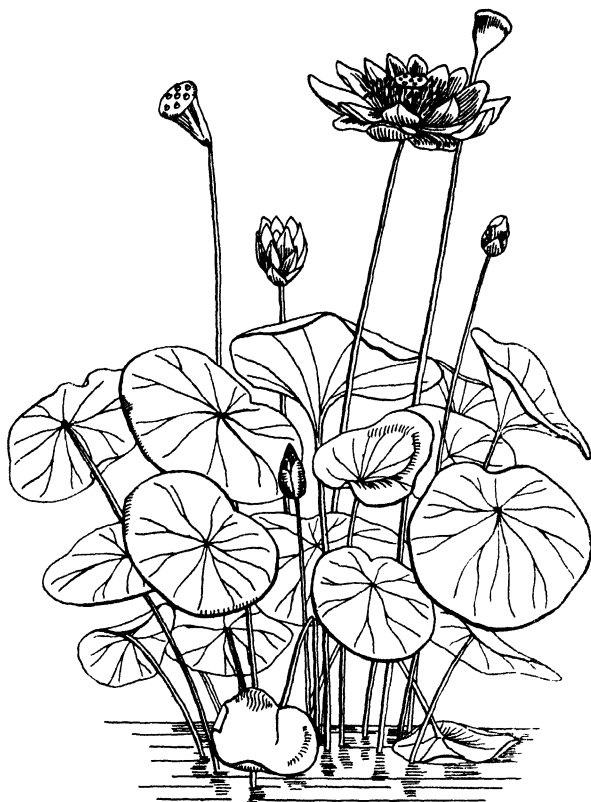


FIG. 65.—*Nelumbo nucifera*, much reduced, after Baillon.

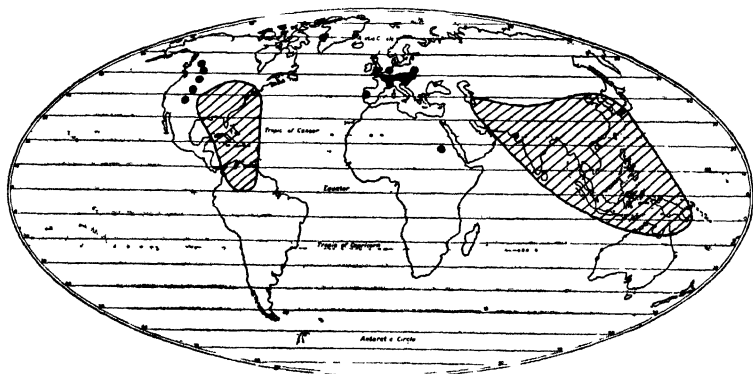


FIG. 66.—Map showing the past (black) and present (shaded) distribution of the genus *Nelumbo*. The evidence for the occurrence of the genus in Greenland is scarcely convincing.

been shorter than any of the others, and remains of it are scarce. They are widely scattered but nowhere abundant, and it is fortunate that those of Europe are complete enough to give a fairly good picture of the period as a whole, because the Pliocene provides some most important links in the history of the Flowering Plants.

The outstanding feature of the period is that, unlike what has been seen before, it illustrates conspicuous floral changes, and these are best realised from a description of successive Pliocene floras.

Particular reference may be made to three fossil floras closely related in space but usually assigned horizontally to the Lower, Middle and Upper Pliocene respectively. The first and oldest of these is the Reuverian flora from the Dutch-Prussian border in the neighbourhood of the Rhine. It contains some 300 species which are of distinctly warmer affinity and type than those now living in the locality, and which suggest a flora not unlike that of the Miocene. There is also, as was noted in the Oligocene, a very marked relationship with plants to-day living in eastern North America and eastern Asia.

The second or Teglian flora also comes from the Dutch-Prussian border and differs from the first chiefly in having more herbs and aquatics and much less affinity with the American-Asiatic flora.

The third or Cromerian flora comes from East Anglia and belongs to the end of the Pliocene. All but about 5 per cent. of its species are identical with those now living in eastern England, and the American-Asiatic affinity is almost gone. Conversely this flora may be described as practically that of the same region to-day.

These floras contain many seeds and fruits and have been carefully studied by the Reids (197), whose work on this kind of plant fossil is so well-known.

The correlation of other Pliocene floras is too uncertain to make possible any real comparison with those just mentioned, but most of them reveal floras very like those of the same regions to-day. The comparatively rich fossil floras of Japan, however, seem to be rather different in that they indicate rather cooler conditions, as appears to be true also of certain other Asiatic floras.

Poor as it is compared with earlier periods, the fossil record of the Pliocene is, nevertheless, sufficient to reveal the most important feature of the time, namely, the comparatively sudden and rapid change in climatic conditions. At the beginning of the period the vegetation, and, by analogy, the climate, remained much as they had been for a very long time and perhaps ever since the Cretaceous. By the end of the period the plants, of north-west Europe at least, were practically as they are to-day, conforming to a temperate or even cool-temperate climate. In short, in many parts of the world the age-old and generalised warm-temperate or subtropical flora had given place in a relatively very short space of time to one of a kind not previously recorded in the history of the Flowering Plants, and perhaps representing climatic conditions equally unprecedented.

This alteration marked the beginning of the catastrophic change and deterioration in world climate which culminated in the extensive glaciations or "Ice Ages" of the immediately succeeding Pleistocene period, but before considering this very important phase in the history of the Flowering Plants it is worth while to summarise what has so far been said.

All the available evidence points to the fact that the Flowering Plants, from the time that they first appeared somewhere in the earlier part of the Cretaceous right down to the middle or end of the Pliocene, pursued the even tenor of their way

without encountering any serious problems or difficulties in the nature of rapid environmental changes. Throughout this long period their history seems to have been that of a group of organisms gradually broadening and differentiating by the multiplication of forms, in the course of secular time, and coincidentally attaining a more and more dominant position among the vegetation of the world as a whole. Environmental or, at least, climatic differentiation, with its attendant morphological differentiation, seems to have been at a minimum, and the fossil record certainly suggests that, at any rate in the higher latitudes of the northern hemisphere, there was one almost ubiquitous flora, reaching, it may have been, even to the highest latitudes. Then quite rapidly at some time during the Pliocene this idyllic sequence was broken by a drastic deterioration in the climates of the higher latitudes, culminating in widespread glaciation and presenting to the plant world problems of environmental harmony which it had never before encountered.

The Ice Ages

By far the longest part of Angiosperm history has now been covered, and what remains is almost infinitely shorter, but this is more than compensated for by its exceptional interest and significance. This may be expressed by saying that the first part is a history of prosperity; while the second is a history of adversity and difficulty. With the Flowering Plants as with other things besides plants it is the latter which is the more revealing.

The study of the Pleistocene and its Ice Ages is so complex and there is so enormous a literature about it that it can be dealt with here only in the merest outline and only in so far as it directly concerns the subject of plant geography. Much of all the available information has been collected together by Wright (268), and this, supplemented by the work of Antevs (6), is the source of much that follows.

As a preliminary it is of value to distinguish between the two most striking effects of glaciation, the formation of glaciers and of ice-caps, because although the difference between them is one of degree only, it is a matter of some importance here.

Glaciers are commonly to be observed to-day in elevated regions at almost all distances from the poles and may be described as frozen rivers filling the upper valleys between the mountains. They are usually more or less distinct entities, and they are normally overtopped by uncovered mountain peaks.

When and where, however, the effects of intense cold are sufficiently accumulative, the individual glaciers tend to lose their identity and to coalesce into huge masses or caps of enough bulk to over-ride and cover all land elevations and to form great ice-fields. These are known as ice-caps. In their typical form they are found only in the polar regions.

To-day there are in the world only two major ice-caps, one in the north covering Greenland, and one in the south covering the whole of Antarctica. There are certain other minor caps, especially in the north.

Glaciers, on the other hand, occur to-day wherever the altitude is enough. They are present even on the summits of high equatorial mountains, and are increasingly abundant in higher latitudes.

When for any reason the temperature of the world falls, the ice-caps increase in size and area and the glaciers become not only more numerous but extend

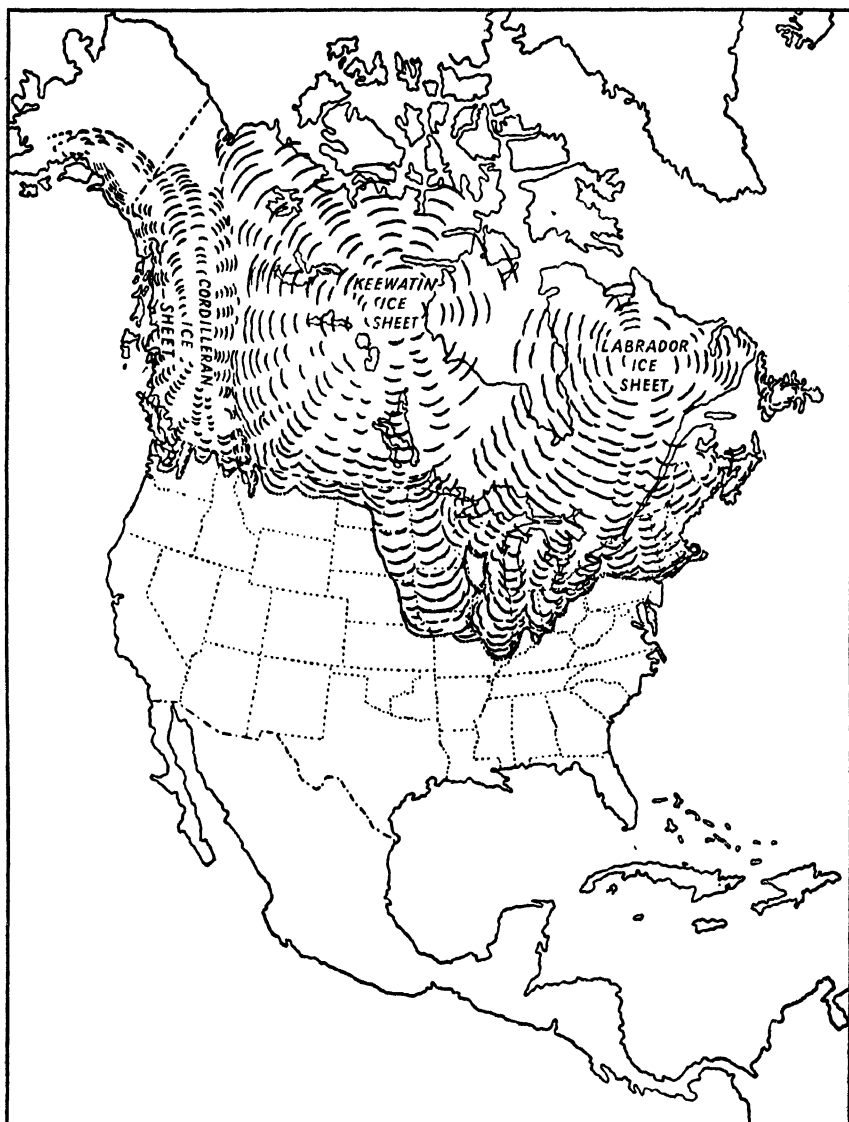


FIG. 67.—Map showing the extent of the ice advance in North America during the maximum glaciation, after Chamberlain and Salisbury.

down to lower levels, often coalescing in the process. Conversely, with a rise of temperature the area covered by ice contracts. The measure of the intensity of glaciation at any time is thus the size of the ice-caps, namely the latitude to which they extend, and the level to which glaciers descend. Since it is only natural to regard the present state of affairs as a norm or mean, the term Ice Ages has thus become applied to such times as the caps and glaciers extended appreciably beyond their present limits.

It is now known that the Pleistocene consisted of more than one glaciation, that is to say that the amount of ice increased and diminished more than once in accordance with climatic oscillations, but there is some doubt still about the exact sequence of events in the different parts of the world. There are evidences of extensive glaciations in the southern hemisphere as well as in the north, but there is, in particular, much variance of opinion as to whether these glaciations were synchronous with those of the north. On the whole the evidence seems to suggest that they were.

In any case the distribution of land and sea in the two hemispheres and the remoteness of the Antarctic continent have made the traces of glaciation much more conspicuous in the north, and there is an inevitable tendency to regard the effects of glaciation as being much more marked in the north than in the south. This is probably quite unjustified, and Skottsberg (224) has corrected the impression graphically when he says "the disappearance of the Tertiary antarctic flora during the ice ages is of fundamental importance and has been greatly underestimated by plant geographers. No catastrophe of such dimensions and of such consequences has ever befallen the Tertiary flora of the northern hemisphere."

The course and sequence of the Pleistocene ice ages have been particularly studied in the Alps by Penck and Brückner (182), and it appears that here at least there were four successive glaciations of different intensities and that these were separated by interglacial periods during which the climate returned to more genial values, such as are familiar to-day (212) (fig. 69). During the glaciations the glaciers crept down the valleys, and during the interglacials they retreated. Fortunately glaciation leaves behind it, in the form of striated rocks, moraines, eskers and drumlins, fairly clear evidences of its course, and from these it is possible to learn a great deal about the different ice advances.

The first advance of the ice is called the Günz glaciation and was of medium intensity. It was followed by an interglacial during which the climate probably reached values rather higher than those of to-day. The second glaciation is the Mindel, and this again was followed by a similar but much longer interglacial. During the Mindel the ice probably reached its maximum extent. The third glaciation is called the Riss and seems to have been of lesser extent than the one preceding it. It, again, was followed by a third interglacial period, from which several interesting fossil floras are known, indicating a climate slightly warmer than the present. Finally there was the Würm glaciation, less intense than any of its predecessors, and this was followed by a gradual improvement of climate to the condition that we know to-day.

The question next to be considered is whether the sequence of events in the Alps occurred also elsewhere. It can only be said here that while the fourfold classification and nomenclature just described were made with special reference to the Alps, there is reason to believe that a similar if not exactly synchronous series of glaciations occurred in other parts of the northern hemisphere.

In the Alps the glaciations concerned a relatively small complex of glaciers, but

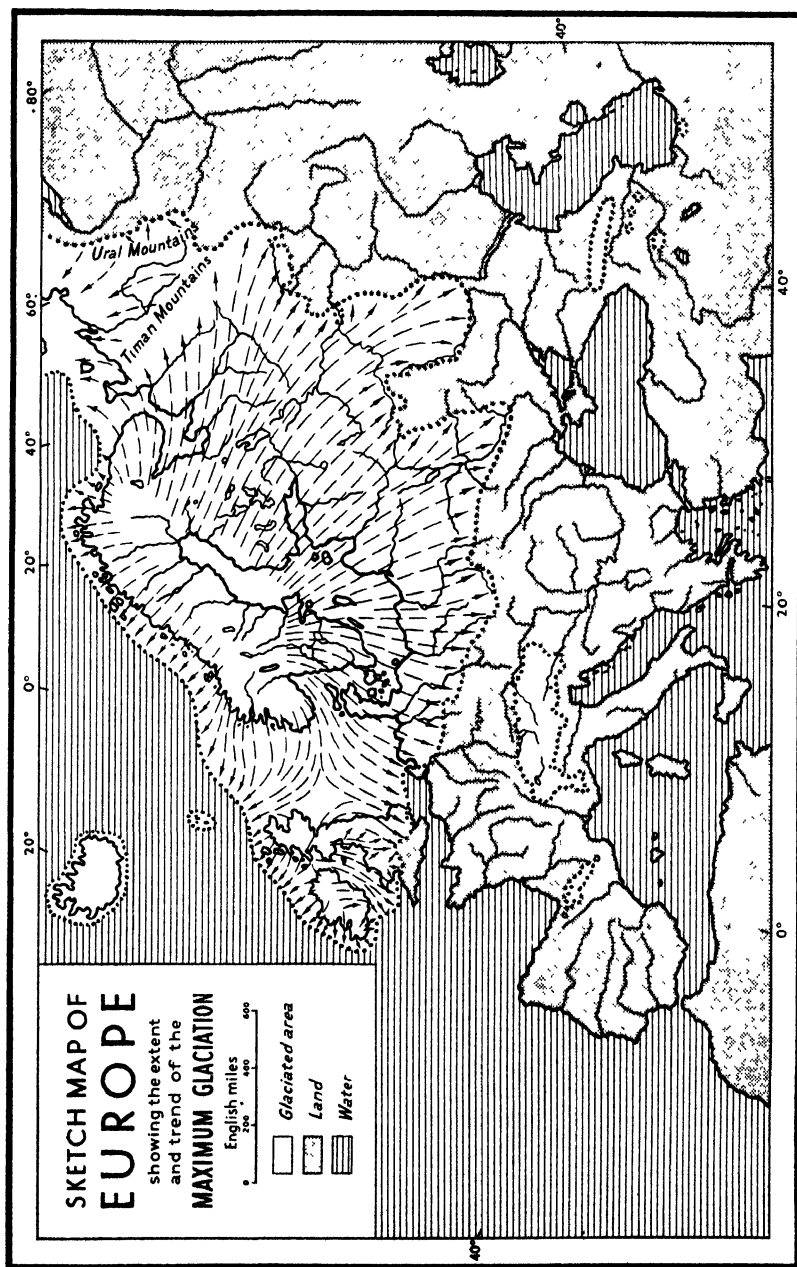


FIG. 68. Map showing the extent of the ice advance in Europe during the maximum glaciation, after Chamberlain and Salisbury.

in higher latitudes it was the polar ice-cap itself that waxed and waned, and what in the former case was but a local lowering of the snow line, in the latter took the form of great latitudinal extensions of the ice-cap. During the first glaciation the spread of this ice south was relatively small, covering Europe only in its most northerly parts. It was in the second glaciation that the polar ice attained its maximum extent, and the limits of this must be discussed in some detail.

It might be anticipated that the ice would extend in all directions south from the present poles, but for reasons which are not altogether clear this was not so, and the actual centre of the northern ice-cap during the maximum glaciation lay somewhere near the middle of Greenland. Because of this the glaciation most affected North America, and here the cap's southern edge (figs. 67, 68) followed approximately the present frontier of Canada in the west and the latitude of 40° N. in the east. Passing to Europe, the edge was so situated that the whole of Ireland was covered and all Britain as far south as a line joining the Severn and the Thames. Thence the edge extended almost straight across the continent to a point some distance north of the Crimea, and from here it ran, with certain marked indentations, to pass out into the Arctic Ocean along a line somewhat east of the Ural Mountains. Thus scarcely any part of Asia was covered by the cap, but the glaciation of the mountain masses in that continent was much greater.

The greater extent of this maximum glaciation obscures to some extent the details of the others, but it is thought that the third glaciation was comparable to the first in extent. The fourth, which is the most problematical, was apparently markedly smaller than the others. As in the Alps, the glaciations were separated by interglacial periods of improved climatic conditions, but the details of these periods are not yet very well defined.

It will be readily appreciated that the amount of ice contained in the caps during the glaciations must have been enormous, not only in bulk but also in weight, and that with variation in the caps there must have been corresponding differences in the weight of the ice resting on the surface of the earth. It is probable that mainly to this must be attributed the many changes in the relative level of land and sea so often found associated with glaciation. But besides the actual effect of weight, a single glacier or arm of an ice-cap may often have had the effect of damming up the normal drainage of an area and causing the imprisoned waters to rise to a much higher level than would otherwise have been the case. Changes of these sorts have doubtless played an important part in plant geography.

For a long time after their recognition it was supposed that the ice ages of the Pleistocene formed an isolated phenomenon in geological history, but it is now known that this is not so. There have been in the whole course of geological history several glacial epochs, but these have been separated by immense periods of time and they are for the most part so remote that little is known of their details. Even the one before the Pleistocene was as far back as the Permian period, many millions of years before the Flowering Plants came on the scene at all. Here, therefore, we need take notice only of the Pleistocene glaciations, although the fact that there have been others is of considerable theoretical importance.

One of the most important recent developments in the study of glaciology has been the success attending some of the attempts to arrive at an actual chronology



Plate 19 Nipa Palms in Java

(from Karsten & Schenck Vegetationsbilder)

of the Pleistocene, and especially of the latter part of it. In the case of the Alps, for instance, actual figures, compiled from many lines of evidence, have been mentioned with some confidence. Penck (182) has made a curve to a time scale for the whole period (fig. 69), also indicating the rise and fall in the snow line, that is to say in the general level of the ice.

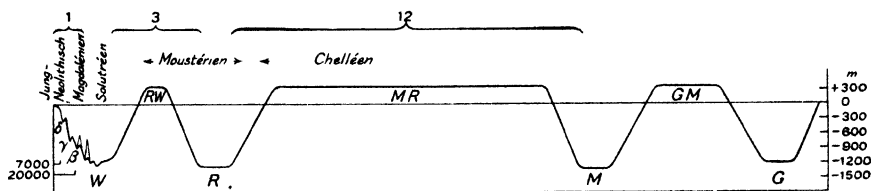


FIG. 69.—Graph showing the variation in temperature in the Alps during the Ice Ages, after Penck and Brückner.

According to this curve something like half a million years have elapsed since the end of the Pliocene, and nearly half of these are occupied by the long interglacial period between the Mindel and Riss. Twenty thousand years is suggested as the time covering what is called the post-glacial period, that is, the time since the latest (Würm) ice-cap began to retreat. It will be noted that this last rise of the curve is shown as a number of steps. Probably all the curves should be drawn in this way with minor oscillations, but it is only in this latest phase that these are sufficiently well known to be recorded. The shortness of the post-glacial period is one of the most interesting features of the curve. Twenty thousand years is a long enough period, but compared with the usual measures of geological time it is almost inappreciable and brings the fourth glaciation almost within sight, as it were, of the present.

This chronology is supported in general by other and different estimates. One of the best-known is the rate of movement up stream of the Niagara Falls, which have existed only since the retreat of the fourth ice-cap. Here the figure is about 25,000 years. The most striking figures, however, are those obtained by De Geer (53) and others from their studies of the laminated clays or *varves* of southern Scandinavia. Details of these studies must be sought elsewhere, but it can be said here that from them it would appear that a period of some 14,000 years has elapsed since the southernmost part of Sweden began to be uncovered by the retreating ice, and that about 9,000 years have passed since the neighbourhood of Stockholm was uncovered.

The study of these laminated clays is but one instance among many of the way in which Scandinavian scientists have taken advantage of the features of their country to make themselves pre-eminent in the study of problems relating to glaciation. Another line of research that has attained great proportions far beyond the land of its birth is in the investigation of post-glacial and, to a lesser extent, other floras by pollen analysis (34, 88, 280). Peat, which may be called a peculiar sub-fossil state of plant remains, normally contains great numbers of pollen grains of the plants which lived during, and contributed to, its formation, and by treating samples of peat in a special way it is possible not only to examine this pollen but to identify it. Peat has been forming for much

of post-glacial time, and this method correlated with others has enabled a good account of the vegetational changes consequent upon the retreat of the ice to be drawn up.

It appears, as might be expected, on other and less direct evidence, that there followed in the wake of the retreating ice a series of floras or vegetation states each more temperate in character than the one before it (286). In Scandinavia in general five main stages are recognised in this gradual re-immigration of the flora (4). The first plant-cover after the actual departure of the ice was an arctic one, but this was soon followed by a flora in which the birch was dominant. This in turn gave place to coniferous forest, which was itself followed by deciduous forest in which oak and hazel were outstanding constituents. Subsequently there was a further stage in which beech was prominent. More recently still there seems to have been some additional fluctuation in the form of a slight recurrence of earlier conditions, and a final recovery to the present state.

These stages have been recognised in whole or in part in many parts of the glaciated regions (see Chapter 12). In Ireland, for instance, a very important point was first brought to light, namely the existence of a post-glacial climatic optimum, that is to say of a time when climatic conditions were actually rather better than they have ever been since. This optimum has also been particularly well demonstrated in Scandinavia in the case of the hazel.

The immigration which has been described above in terms of its chief plants is also commonly classified according to its prevailing climates (see p. 204). First there was a pre-boreal stage with an arctic flora; then a boreal period comprising the birch and conifer stages; next an Atlantic period, when the climate was more oceanic and when there was deciduous forest; and finally two minor phases, the sub-boreal and the sub-Atlantic, comprising the most recent minor oscillations.

Brief as the foregoing account of the Pleistocene is, it is enough to show what a profound effect this period must have had on the vegetation of a great part of the world. Whether or not previously there was local glaciation on the summits of high mountains is a question which will be discussed in a later chapter, but there can be little doubt that the arctic conditions (widespread glaciation at sea level) which characterised the period were conditions never previously experienced or encountered by the Flowering Plants, and that many of them were, as a result of them, faced with the necessity of adjusting themselves to influences of a quite novel kind. Further than this, the effects of the ice were greatly intensified by the catastrophic speed at which it came and by the series of oscillations that accompanied it. The significance of the speed of glacial onset in particular requires to be fully realised. Previous to the later part of the Pliocene the speed of morphological evolution in the Angiosperms may be pictured as being faster than and perhaps unrelated to climatic change, or, to put it differently, the plants may be pictured as changing by the processes of evolution more rapidly than their surroundings, so that quite possibly the problem of adaptation, as the term is understood to-day, did not arise. With the coming of the Pleistocene glaciations this relationship was entirely altered. Climatic change was accelerated to such a pitch that by no stretch of imagination can it be supposed that evolution was able to keep pace with it, and there thus arose a situation in which the environment was changing much more rapidly than its inhabitants. Again in somewhat different phrase, environmental change completely outran evolutionary change. The result in many parts of the world was a state of stress between organism and

environment such as may never have occurred before. In short, if these suppositions be correct, the effect of the ice ages on the Flowering Plants was completely to upset, over much of their range, the balance between plant and habitat. Since there has not been, in the time which has elapsed since the fourth glaciation, any appreciable restoration of pre-glacial conditions, the botanists of to-day are studying a world vegetation but lately subjected to a devastating disaster. The study of the geography of the Flowering Plants is peculiarly the study of the consequences of this disaster, and this being so, the outstanding importance of the Pleistocene in relation to the general story can scarcely be overestimated.

PART TWO

CHAPTER 15

THE FACTORS OF DISTRIBUTION—I. GENERAL REVIEW

THE first part of this book described the facts of plant geography: and the purpose of this second part is to consider the possible explanation of them. The following chapters therefore first discuss what are usually called the "factors controlling plant distribution," and then try to determine how far and in what manner these may, in combination, be considered to provide a general explanation of the distribution of plants as it is to be observed to-day.

The factors of distribution can be grouped under a small number of main headings, to each of which a later chapter is devoted, but much is to be gained by a general and comprehensive preliminary survey showing more clearly the mutual relationships and values of the various factors.

In the widest sense the distribution of plants to-day is the effect not only of natural causes but also of artificial ones, namely those which operate as a result of the intentional or unintentional activities of human beings. With these human factors this book is not, to all intents and purposes, concerned, although it is necessary on occasion to refer to some of them incidentally. Its theme is rather the natural distribution of plants, and for this reason the influences of man, though often intense and widespread, receive little or no attention except in so far as they can be made to illustrate or explain more natural processes.

One natural factor of distribution is so fundamental that it underlies all others. This is the evolutionary factor, which arises from the circumstance that the plant world of to-day has gradually developed from pre-existing forms of plants by those manifold processes which are called "organic evolution."

The basic characteristic of nature as a whole is that its history has been one of slow evolution over an immense period of time, and a proper understanding of the effects and implications of this is so essential for the consideration of any biological problem that the matter was referred to as early as Chapter 3, even before the facts of plant geography had been cited. It is necessary here, therefore, only to emphasise once again the degree to which the evolutionary factor is, as it were, a master-factor, determining in one way or another the operations and results of all those others that have now to be reviewed.

Evolutionary factors may be regarded as inherent or predisposing factors. The more direct factors next to be discussed may be regarded more as potentials or as variables which may or may not influence plant distribution. They represent variable conditions under which plants live and which may become decisive in determining the range of species.

The ordinary flowering plant lives its whole independent life with its roots in the soil and with its remaining parts exposed to the atmosphere, and that it is incapable of movement during this long phase of its existence must always be remembered as one of the main factors in phytogeography and one of the chief ways in which it differs from zoogeography.

In fact this immobility is far more fundamental than is usually admitted, and indeed ranks next to those inherent evolutionary factors just mentioned. The reason is clear. Whatever our views may be about the actual origin of new species, such forms when they first arise must occupy an extremely limited area, perhaps no more than the space covered by a single individual, and their attainment of any appreciable range must be a matter of the actual movement of individual plants.

This being so, the likelihood of any range being attained depends upon the ability of the plant to move at some stage or another in its life history. The question of the average ability of plants to move will be discussed more appropriately later. Here we are concerned only with the axiomatic statement that if the individuals of a species have no mobile phase, the species itself cannot attain a range, no matter how favourable other factors may be.

There are not likely to be many plants without the power of mobility, for the reason that such a disability will function very much as a lethal factor, and we may therefore assume that all plants which do attain an appreciable range possess at some stage in their lives some degree of mobility. What that degree may be will be seen later.

Plants are normally in contact with their environment in two rather distinct directions. Their aerial parts are in contact with the free atmosphere and their terrestrial parts are in contact with the soil, but the latter is really a complex, since it comprises not only the solid constituent of the soil, but both the water and air in the soil. Even this is a simplification of the position, though it is sufficient for immediate purposes.

The conditions of the atmosphere and of the soil vary greatly from place to place and are indeed rarely constant over any considerable area, so that climatic as well as soil conditions are variables obviously likely to affect the distribution of plants in ordinary circumstances. Naturally if all plants were capable of existing under all known conditions, then the effect of these conditions as factors in distribution could at least be no more than secondary, but as far as is known no plants are capable of such existence, and hence these variables are normally direct factors of distribution.

The complex of atmospheric conditions which is usually called climate is generally classified with regard to plant distribution into four components. Most fundamental among them is heat, that is to say the temperature of the air, because it is a direct function of the shape of the earth and its position with regard to the sun. Its actual value from place to place is controlled by various secondary considerations, but these, which will be referred to in due course, have seldom more than a local influence.

Next in importance to temperature comes moisture, most familiar in the form of precipitation or rainfall, but expressed also in the form of humidity, dew and snow. The distribution of moisture values differs essentially from that of temperature, in that it is local rather than general and depends upon local combinations of circumstances rather than upon world-wide conditions. That is to say, moisture conditions are not necessarily bound up with heat but tend to vary widely at all temperatures.

Besides these two primary climatic variables there are at least two others which are important secondarily. These are light and wind, and they are to be regarded as secondary because they exert their influence by modifying the two primary variables of temperature and precipitation. This relation is clearly seen

in the close correlation between light and heat, both being directly due to the influence of the sun. Similarly there is the relation between heat and humidity of the air, which in turn controls the likelihood of precipitation. Finally, both temperature and precipitation are controlled to some extent by wind or air-movement, since this influences both the accumulation of temperature and the accumulation of humidity.

Actually light is probably the least important component in relation to the *distribution* of plants, since, except in the highest latitudes, its mean value and duration seem sufficiently great to preclude it from acting as a limiting factor in plant life. Locally, however, and especially when itself controlled by still more minor conditions, it may be of some importance.

The potentiality of wind as a factor in distribution lies chiefly in the manner in which it may modify other climatic values, and its effects upon temperature and precipitation have already been mentioned. Besides these, however, it may have a more direct influence by facilitating or impeding the proper functioning of the plant at certain particular phases of its life history, or by militating against the attainment of normal growth form.

In contrast to climatic factors, the variables influencing the plant either potentially or actually through its physical contact with the soil in which it grows are usually described as edaphic factors, and here again there is considerable complexity and interrelationship—so much so that it is not easy to arrange these edaphic factors in any very definite order of importance, and the sequence in which they are mentioned here does not imply any such relative value.

Generally speaking, edaphic factors are regarded as comprising three components—the physical nature of the soil, the chemical nature of the soil, and the topographic or physiographic character of the habitat. The first two may be regarded as absolute features, but the third is chiefly of importance as a modifying influence, conditioning not only the first two but also at least some of the climatic factors mentioned previously.

Almost all physiographic conditions may affect a locality as a potential plant habitat, but in the main the two important considerations are altitude and exposure. The effect of altitude has already been dealt with fairly adequately in the chapter on world geography, and it is sufficient to remind readers here that it has a very important influence not only on temperature but also on precipitation, and in fact tends to influence these values in the same kind of way in which they are influenced by latitude.

Exposure is important owing to the way in which it may intensify or diminish the influence of other factors. For example, the detailed relief of an area may profoundly influence the effect of climatic and edaphic factors upon the area according to the degree in which it provides shade or shelter. Slope is also important, since it may obviously influence the effect of precipitation or the effect of insolation. The prevalence of cloud also is often a matter of topography and may lead to a considerable modification of temperature values.

It is seen, therefore, that in so far as the life of the plant is passed in contact with the atmosphere and the soil, variations in the values of these surroundings must almost inevitably react upon the life of the plants exposed to them, and therefore that climatic and edaphic factors must always be among the chief factors in distribution. How far this is true and the general effect of it on the total picture of plant distribution will be seen later, but meanwhile the reader may be referred to a general discussion of the problem by Pearson (181).

We are justified in assuming for the purpose of studying plant geography that every species possesses some powers of extending its range in the sense of being able, when circumstances permit, to multiply the number of its individuals and thereby to cover a greater superficial area. Granted this, it follows that there must be for every species a maximum potential area of range representing that proportion of the world's surface which it may hope to cover in the course of time and by means of its powers of mobility.

This conception is a very important one, because it clearly indicates the part which climatic and edaphic variability may play in determining this potential area. If we imagine a species to be entirely uninfluenced by climate or soil, it is obvious that it is potentially of cosmopolitan range as regards them. There may, of course, be other factors which will restrict its potential area, but they will not be climatic or edaphic. Thus the main rôle of these variables must be to determine the potential maximum area of a species.

Suppose, for instance, that a species is unable to maintain itself in presence of frost, then clearly the potential range of that species consists only of those parts of the world where frost does not occur. Whether it will in time come to inhabit all such places depends on many other considerations, but its relationship to frost does lay down a range beyond which it cannot extend.

Thus the rôle of what have been called the climatic and edaphic factors of distribution is primarily that of determining the potential areas of species, that is to say, how much of the world's surface each species may come to occupy in the course of time if its spread is unopposed. At any rate this is the most convenient way in which to regard these factors and to fit them into the general scheme of plant geography.

The convenience lies in the fact that it points the way towards a useful understanding of other factors which also play a part in determining the distribution of plants, and which in terms of what has been said clearly do so by influencing the ability of plants to attain their potential areas as determined by their relation to climatic and edaphic factors.

Since the attainment of range can only be brought about by the mobility of individuals, it follows that no range at all will be achieved if the individual is completely immobile, and mobility must therefore clearly be the primary factor, at any rate in the facility with which a species will attain its maximum range.

As a broad generalisation it may be said that no flowering plants are capable either of transporting themselves from place to place or of being so transported during their active vegetative life, because their physiology necessitates a permanent association with the substratum in which they grow. The only exceptions are certain plants in which this does not prevail, or rather where it is of a very special character, as, for instance, among small free-floating aquatic plants. Except for these, flowering plants may be regarded as completely immobile during their active vegetative phases.

How then is their movement accomplished? The answer is that in all normal circumstances the reproductive processes of the flowering plants incorporate a phase during which the offspring of one generation can survive separation from their parents and during which their physical attachment to their habitat is severed. This is the seed phase, during which the dissemination or scattering of offspring from the point occupied by the parent occurs. In some plants the production of seed is replaced by the production of such small vegetative parts as bulbils, but these possess the essential feature of seeds, the ability to pass through a dormant

period during which they are capable of being spread over the surface of the ground. This process of "dispersal," as it is more shortly termed, is thus of supreme importance in the distribution of plants and must rank as one of the fundamental factors (203, 287). It is appropriate therefore that we have already found place for it as a general process, but here we are considering more particularly its relative value in assisting species to attain their maximum distribution, and thus it is really to be regarded as a factor of distribution in two rather different senses. In the one sense it is quite fundamental, since without it no extension of range can take place; in the other sense its relative value as between different plants is also of great importance and must be regarded as one of the main factors in determining how easily and rapidly extensions of range may take place.

The actual means by which plants achieve adequate dispersal will be surveyed later, but mention of the process in general is essential here because it bears directly upon the importance of the next factor to be considered. This may, for the sake of a brief title, be called the factor of "barriers."

If dispersal is the only means by which range can be attained, much obviously depends upon the facilities with which such dispersal can operate, and there are likely to be factors which will react either beneficially or harmfully on the process. We need not concern ourselves with the former, because they can only intensify existent powers of dispersal, and we may therefore confine ourselves to recognising what causes are likely to result in an opposite effect. In other words, what are likely to be the obstacles to effective dispersal?

First it is necessary to try to gain some impression of what is meant by the phrase, which has just been used, "adequate dispersal." It is a well-known fact that species differ very much among themselves in the degree to which their seeds and fruits possess characters calculated to facilitate dispersal. We must, of course, be cautious in approaching this subject, because at best we have only a human estimate of these characters, but it is usual to regard certain structural features in seeds or fruits as providing their possessors with what are called "dispersal mechanisms," which increase their dispersal potentialities.

There is no doubt that some seeds and fruits possess features which habitually cause them to be dispersed over greater distances than others, and it is tempting to assume that these plants have an absolute superiority in the matter of dispersal, but this view is based upon a quite unwarranted assumption and its truth is not borne out by observation in the field. The false assumption is that wide dispersal is in a biological sense superior to, or more valuable, than narrow dispersal. It cannot, of course, be denied that there may be occasions in which wide dispersal may be of enormous importance, and examples of this will be mentioned later, but to assume it is certainly unjustifiable. Indeed, there is one consideration which is strong presumptive evidence to the contrary. This is the fact that wide dispersal must have a general tendency, not present with restricted dispersal, to carry the disseminules (to use a convenient term comprehending seeds, fruits or vegetative parts) into regions where the conditions of climate and habitat are likely to be very unlike those from which the parent plant came. In other words, wide dispersal will take the disseminule further but it is very likely to increase the chances against its survival and establishment when it arrives at its destination.

As to the value of specialised dispersal mechanisms, it need only be said here, and it can be said quite categorically, that there is no real evidence that species possessing such mechanisms are more widely distributed, that is to say, have more extended ranges, than those without such advantages, and there is nothing

to show that exceptional dispersal methods result, in general, in exceptional ranges.

Confusion of thought on this point seems to arise from a mistaken conception of the purpose of dispersal. It is perfectly true that dispersal leads to the attainment of range and is in fact the only means towards that end, but it by no means follows that this is necessarily its only purpose, and, indeed, from a biological view it is difficult to imagine that this can be so. Its primary purpose must surely be something more intimately connected with the successful maintenance and survival of the individual plant which in due course will reproduce, and it is not difficult to see what this may be. The immobility of a flowering plant means amongst other things that its offspring will, unless subjected to some degree of dispersal, fall to the ground more or less vertically from their points of origin and will thus come to lie in the shadow of the parent. In some cases, and especially with some types of growth-form, they may not even reach the ground but will be intercepted by the lower parts of the parent. Such hazards are least apparent in ephemeral annuals where the whole parent tends to disappear almost as soon as the ripe seeds are borne, but these plants are by no means conspicuous in range or abundance of individuals, and do not alter the view that in most plants this problem of what may be somewhat picturesquely called "botanical overlaying" is a very real one. May it not, therefore, be that the primary object of dispersal is not to spread the species in the sense of appreciably extending its range but to give the disseminules the best chance of survival by scattering them outside the immediate shadow of the parent?

Whether this is so or not, it is certain that we must regard many of the most widely distributed of flowering plants as having attained their ranges in the course of repeated but comparatively restricted dispersal.

This view leads to what is certainly an important consideration in the total efficacy of dispersal, namely the frequency with which it is repeated. Of two plants with similar dispersal potentialities the one with the greater frequency of reproduction will obviously, other things remaining equal, attain a given range more rapidly than the other. That is to say, the shorter the generation in the species the more frequent will be dispersal and the greater the total area covered in a given time. Contrast, for instance, a plant of chickweed with an oak. There is no need to attempt to estimate their relative powers of dispersal, but it is perfectly certain that the oak will have to be dispersed a very long way at its first reproduction to make up for the large number of generations of chickweed which have passed while the oak was attaining its reproductive condition.

At first sight it may be supposed that in cases of this sort, involving large perennial plants, when once the reproductive age is attained the annual or more frequent production of seed will remove much of the disparity. This is, of course, not so, because in such perennials the seed is produced each time at the same spot and dispersal is not accumulative. It will in fact not be appreciably increased until the offspring of the original tree have themselves reached a reproductive stage. Another very significant consideration in dispersal is the length of time that the disseminules remain viable and capable of germination, because it is obvious that the longer a seed remains alive the more time will the various dispersal factors have in which to make their influence felt, and the greater therefore will be the likelihood of wide dissemination. Viability, especially in relation to seeds, is a wide subject, and readers who desire further information about it may refer to a summary in which most of the relevant information is considered in one fairly

short article (50), but it is worth while noting that the life of many seeds is considerably shorter than is generally supposed, and that the oft-reported germination of seeds from ancient tombs and similar situations has never been substantiated.

We must now return to the question of "barrier" factors, but our digression has not been without value, because it will help us to estimate what may or may not constitute a barrier to dispersal. It will be remembered that we were concerned to discover what might be meant by "adequate dispersal," and it will now be seen that there is good reason to regard it as anything which scatters the disseminules so effectively that they can begin their germination unhampered by the presence of the parent. How does this affect our conception of barriers?

By a barrier (using the term in its phytogeographical sense) is clearly meant something which cannot be surmounted by the only process of movement open to plants, namely dispersal, and it is possible to imagine one or two very different kinds of such barriers. For instance, it is conceivable that purely local conditions might be such that the ordinary methods of dispersal would be unable to operate, as might easily happen to an individual in such a position that its disseminules are actually and physically prevented from scattering sufficiently to allow them to germinate. Here the normal dispersal of the individual is interfered with.

Much commoner and indeed the usually accepted type of barrier is one which, rather than interfering with dispersal, simply tends to make it nugatory. In short, "barriers to dispersal" are considered in a general sense as comprising areas of such a kind and extent as cannot be crossed by the spreading species in the ordinary processes of its dispersal. Two components are obviously involved, the one being the nature of the area and the other its size. Potential barriers of this kind are therefore provided by any areas where conditions are so unsuitable for a particular species that its disseminules, when scattered into the area, cannot germinate. This is a general statement, but clearly the actual barrier value of any area to any given species must depend upon the dispersal potentialities of that species.

This leads to what is perhaps the most important general conception with regard to barriers, that they are seldom to be regarded as complete barriers to the dispersal of every plant. It is true that the very largest areas will tend to be so, but even here one has to reckon with the possibility of accidental dispersal across them, and in usual terms barriers should be recognised as likely to be of very varied significance according to the different plants in whose path they lie.

In the present circumstances of world geography potential barriers may be either land surfaces or water surfaces. These differ rather fundamentally in relation to the Flowering Plants, in that the nature of the obstacle presented by the former will tend to depend upon a variety of circumstances, while the latter will tend to be absolute obstacles in almost all circumstances except in the case of accidental circumvention.

Hence the distribution of land and sea in general must also be regarded as one of the important factors of distribution. As regards land barriers, these may be of very varied nature according to the plants associated with them, and, what is most important, they tend to have a marked segregating effect. Many areas, for instance, may act as barriers to the dispersal of some species while permitting the dispersal of others, while some barriers will be complete obstacles to most if not all species. It is therefore almost impossible to generalise about them, and each must be considered as a law unto itself. It can, however, be said that the more homogeneous an area the smaller or fewer the barriers it will present, while the more

heterogeneous it is the more complete and numerous the barriers it will contain. For example, if two regions with very different climatic or edaphic values adjoin one another, it is probable that each will be a serious barrier to species belonging to the other, because neither is likely to provide the conditions required by species from the other. On the other hand, where the passage of environmental conditions is gradual, so much the less serious are the barriers likely to be. Again, areas in which conditions are extreme in whatever sense are likely to be more serious barriers than areas where the conditions are of more medium values. This is why mountain ranges and deserts are among the most obvious barriers to dispersal. But these are only extreme cases, and it is to be remembered that any area is a potential barrier to the disseminules of species inhabiting places where the conditions are appreciably different.

Nor must it be forgotten that though one geographical arrangement may place barriers in the way of dispersal, a different arrangement of external conditions may facilitate dispersal. This is a very important consideration, because the latter effect is likely to be a focussing of plant movement along certain lines, and there will develop what may be regarded as lines of least resistance along which extensions of range will be especially easy.

This point can be nicely illustrated with reference to mountain ranges. A mountain system running athwart the direction of dispersal of a species is likely to provide a very serious obstacle to its further spread, because the conditions at the higher levels will tend to be very different from those on the plains below, but mountain ranges or systems lying in the direction of dispersal are likely to be valuable stepping stones or pathways, because conditions will tend to maintain themselves throughout the length of the mountains, and even if this is not so, the flanks of mountains usually exhibit so wide a range of conditions in a comparatively confined space that they are almost certain to provide some niches or footholds by which dispersal can be continued.

The question of water barriers, although of even greater absolute importance than that of land barriers, is simpler for two reasons. Except for a few comparatively unimportant exceptions water barriers to dispersal are sea barriers. Large areas of fresh water are nowhere in the world to-day very conspicuous, and none is so situated as to present a barrier of first-class importance. Moreover, the Flowering Plants are, except for the small number that inhabit tidal waters, all land or fresh-water plants to which any considerable width of sea water is almost inevitably a complete obstacle. Certainly there are quite a number of species whose disseminules can withstand prolonged immersion in salt water and which are therefore liable to be transported widely by sea currents, but these are mostly highly specialised strand plants occurring only in the immediate vicinity of the sea shore and do not bulk largely in the constitution of inland vegetation.

As a matter of fact these plants afford an indirect but none the less interesting confirmation of the views on the significance of wide dispersal given above. In their case dispersal by currents is effective not in virtue of the wide distances which may be covered but because the correlation of these plants' requirements with the conditions on sea beaches enables them to germinate and establish themselves successfully there after they have been so dispersed. On the contrary, inland plants are not likely to benefit by current dispersal, first because their disseminules are not likely to reach the sea, and secondly because even if they do so they will not be carried to spots where they can germinate.

Opinions vary considerably as to the extent to which areas of open sea constitute barriers to the dispersal of species living in ordinary inland situations. It may be greatly influenced by the structure of the disseminules themselves, and it is particularly in this circumstance that many so-called "dispersal mechanisms" may possess real and absolute values.

With regard to the problem generally, the case of the island of Krakatau is of much interest and importance, as affording at least a small amount of definite fact. It lies 40 miles west of Java in the Malayan Archipelago, and in 1883 was the scene of a devastating volcanic eruption, as a result of which two-thirds of it was destroyed, the part which remained being generally supposed to have been completely sterilised of living things by lava and ashes. In 1886 visiting botanists found on the island 15 species of Angiosperms, most of them strand plants; at the present day there are 271 species, and Docters van Leeuwen in a recent book (59) expresses the opinion that, of these, 40 per cent. owe their origin to dispersal by wind, some 30 per cent. to dispersal by ocean currents, and 25 per cent. to carriage by animals; only a handful are the result of man's introduction. This work of Docters van Leeuwen is of special interest because it seems to dispose finally of the suggestion (10) that part of the vegetation existing before the eruption survived it. On the contrary, it seems reasonably certain that the present vegetation is entirely new, and hence that in the last fifty years some 250 species have succeeded in crossing at least 40 miles of sea by the ordinary methods of dispersal, and that the island has been restocked with vegetation by this means in a comparatively short time. It is dangerous to argue from the particular to the general, but it seems safe to conclude on this evidence that sea distances of the dimensions noted do not in fact present any considerable obstacle to dispersal.

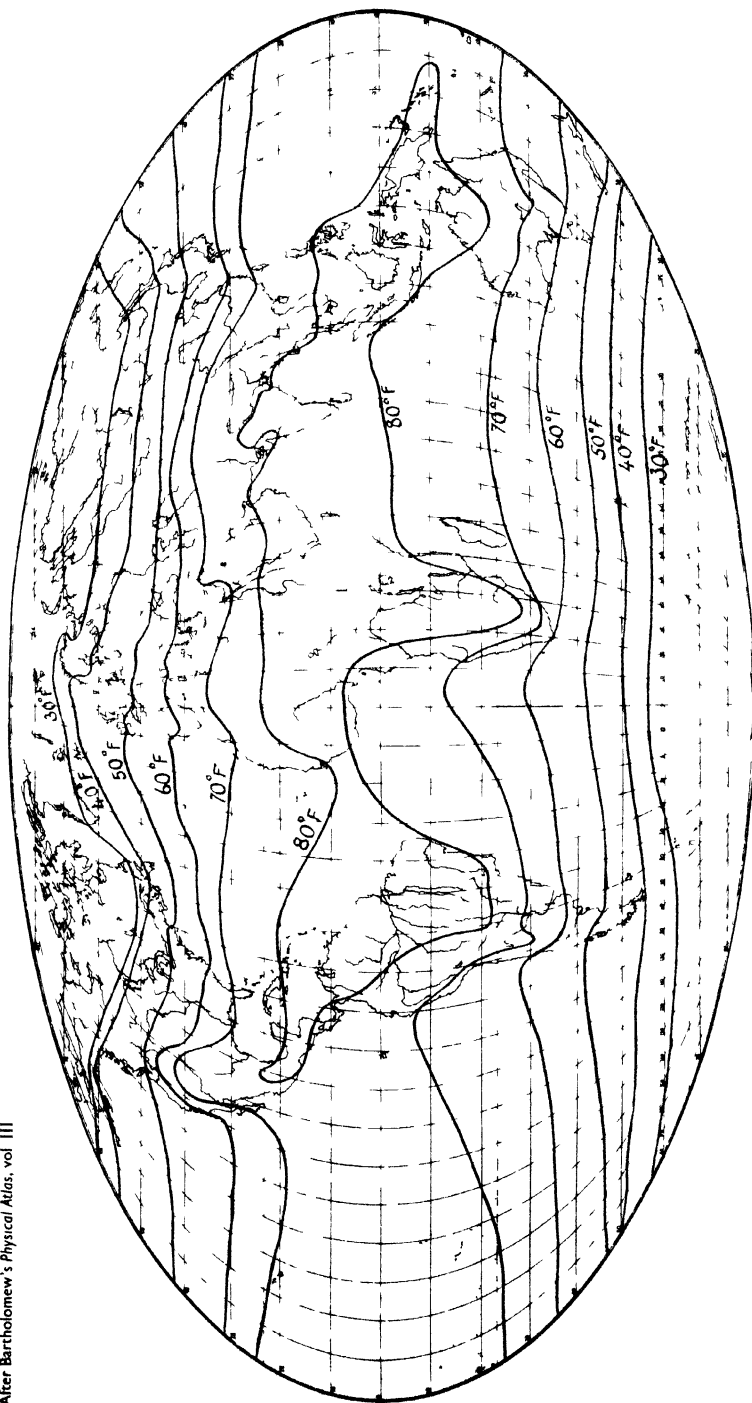
It was pointed out in introducing this discussion on the factors of distribution that these result from and depend upon the fundamental consideration of the development of the organic world by the processes of evolution, and this led to the recognition that time itself must be one of the most basic factors. In that reference to age we were concerned only with its possibilities as determining the actual size of the range of species and other units, and it was regarded chiefly from the point of view of the concepts embodied in the theory of Age and Area, but age, or rather the passage of time, has another most important bearing on plant distribution in that it affects the operation of other factors. It may be expressed as a general assumption that the *status quo* in nature is never maintained for very long, and indeed the whole developmental conception of the cosmos incorporates the fundamental idea of constant if slow change. What the direction of that change may be does not concern us, but the fact of change itself does so intimately.

In relation to our immediate subject it means that factors of distribution must be regarded not as something static and unchangeable, but as something subject to the same influences of time as other aspects of nature. Hence any particular factor must be looked upon not only from the point of view of the present but also of the past, and particularly there must be taken into account changes which the passage of time may have brought about in it, while for each of the factors already mentioned there must be added a subsidiary or supplementary factor incorporating the possibility of changes in the operation of the factor at an earlier time.

This influence of the past is not of equal importance with regard to all factors. Dispersal, for instance, or rather facility for dispersal, is a character of the species

Map of the World showing the distribution of mean annual temperature
After Bartholomew's *Physical Atlas*, vol. III

PLATE 20



Atlas cont. 4. Distribution increasing towards North. 11. P.
Approximate Scale 1:100,000,000 (600 miles 1 inch along Equator)
on Mollweide's Homographic Projection

more often than not associated with morphological features and is not subject to change by the mere passage of time unaccompanied by evolutionary change in the organism. The morphology may in time so change as to influence the dispersal potential, but this will be presumably accompanied by such a change of shape and structures as may constitute the characteristics of a new species, in which case it begins to establish a distribution of its own.

Again we need not concern ourselves especially with changes in edaphic conditions in the past, because these changes are almost exclusively the result of the operation of other factors. Thus changes in climate and changes in topography will usually be the cause of changes in habitat, although there are doubtless many other minor factors on which the nature of the substratum will depend, but there is no particular sequence or series of edaphic changes which is the result of the secular passage of time alone.

There remain the two main factors of climate and barriers, and in both of these the time conception is of such importance that we must regard changes of climate and changes of geography in the past as among the leading factors of distribution.

Changes of climate mean alterations in the distribution of climatic values over the surface of the world. In so far, then, as the potential area of species is determined by climatic considerations it will change in response to any change in climate distribution. To put the matter rather differently, if there is accepted the view that the distribution of climate has changed in the past, then there must also be accepted the view that potential areas of distribution have also changed to a greater or lesser extent and that therefore such climatic changes must be a factor in the present distribution of plants.

The possible importance and significance of geographical changes in the past in relation to plant distribution are even more clearly demonstrated. These geographical changes may be visualised as affecting two geographical features (the outline of land and sea and the distribution of relief), which may be described as geographic and orographic. But these features of geography are, as has been seen, the very features which produce barriers to dispersal, and so it is clear that changes in outline and relief in the past may affect plant distribution very considerably, at least in so far as they may accentuate or diminish the effects of barriers.

Still one factor remains to be discussed, and it is interesting to observe that, like the first one mentioned (the evolutionary factor), it is one which resides in the very nature of the plants themselves and is not directly a factor of the environment, although environmental features may condition its operation. This factor is the factor of competition.

Competition is not altogether a satisfactory term, and it might be better to say the "struggle for existence," which is what is really meant. The existence of disparity between the potential number of individuals and the means for their support has long been a biological axiom. It was first demonstrated in scientific form and language by Malthus in his famous essay on human population (155), but it is most familiar as the basis for the conception of the doctrine of "natural selection," which is the belief that, given such a disparity, there must be a struggle between individuals for the limited supplies, and that victory will go to those best equipped for the battle. This is expressed by the further biological conception of the "survival of the fittest." Whatever may be the validity of this, the occurrence of a struggle for existence and the survival of but a proportion of individuals produced are beyond dispute.

Hence there must always be, as a general concomitant of evolution, that particular aspect of the struggle for existence which, in the plant world at any rate, is usually termed competition. What is really important is to realise that in the circumstances this factor of competition must be a final and decisive one.

It is easy to see the reason for this. The variation in climate over the world's surface is much less than the multiplicity of species which have to live within it, and the same is true of the range of edaphic conditions. It follows, therefore, that there is no possibility of species sorting themselves out geographically in such a way that each will occupy its own niche in space untroubled and unaffected by others. It is true that the degree to which the presence of others will be felt varies greatly according to the circumstances, but it may be accepted that most areas will be open to occupation by more than one species, and more often than not by a large number. The ultimate constitution of the vegetation must therefore depend upon what happens to the different potential constituents, and to what extent each is able to establish itself against and among the others. If one cannot do so at all it will be absent from the area, and thus its total range must depend ultimately on the result of this struggle that we call for convenience competition. In no reasonable circumstances can the absence of this struggle be visualised, and hence it must be the ultimate factor in determining the detailed distribution of plants.

The operation of competition is best illustrated by the stages in the gradual colonisation by plants of an open and suitable piece of ground such as may be provided by a landslide, by an eruption, by rainwash or by the retreat of ice.

Sooner or later the first colonists will make their appearance on the uninhabited area by dispersal from the surroundings, and at first at any rate the number of immigrants will be so small that each to which the habitat is suitable will germinate and grow without any interference from the rest except in so far as accident of position may cause it. Gradually numbers will accumulate until the space available is full and the plants are in actual contact, forming a complete covering. The vegetation is then said to pass from the open to the closed condition. This passage is an important one because it means that henceforth competition in some degree will be the prevailing condition. The mere process of dispersal into the area will not normally bear much relation to the suitability of the immigrants to the habitat, and hence competition is likely, in the earlier stages, to take the form of the gradual elimination of some species by those more suited to the conditions. At a somewhat later stage the competition will become more and more competition between relatively equally suitable species. Those plants whose claim to position is simply based on the act of dispersal will tend to give place to others more in harmony with the actual conditions, until there develops an association of species more or less characteristic for the habitat.

Hereafter the competition will take the rather different form of a struggle between the individuals of a comparatively small number of species, and on the outcome of that will depend the relative abundance and frequency of the different species concerned.

Usually the competition between species as opposed to the competition between individuals of the same or of a few species will not entirely disappear, because with the development of the vegetation there will usually go minor changes in the habitat brought about by the effects of continued plant growth. For instance, decaying vegetable matter will accumulate from the generations which are gone and the soil will tend to become different in a variety of ways. For this reason

there is generally a gradual development of the vegetation in the sense that new combinations of species grow up in addition to the competition between individuals of the same species.

The whole process moves towards an equilibrium which will ultimately be established provided no serious disturbing factors such as climatic or other changes intervene. This equilibrium is reached when the association of species becomes such that the entry and establishment of fresh species from outside diminishes to vanishing point.

Thereafter competition will become entirely a matter of struggle between the progeny of the individuals of the species which form the vegetation. This equilibrium vegetation is called the climax vegetation and represents the highest grade of vegetational development which is possible in the general conditions of the environment. Where the climate is suitable the climax vegetation is usually some kind of forest, and the gradual stages by which it is attained can roughly be described as the replacement of small and herbaceous species by larger woody species, but there are many factors which modify the process and which induce certain degrees of equilibrium short of this condition.

Such is but a very bare account of what is in fact the whole of one very important aspect of the study of plant ecology. Its purpose is merely to show that competition is not one simple process but may take very different forms in varied circumstances. To summarise still more what has been said, the earlier stages of development and plant succession may be likened to the more active and chaotic stages of hostility and struggle from which there gradually emerges the victory of a comparatively small number of forms, which thereafter may be regarded as having attained a working degree of harmony between themselves. It is not supposed that when this is attained competition ceases. It is rather that competition comes to have the rather more limited objectives of maintaining the occupancy of species and of maintaining an appropriate balance between the different species. So long as any appreciable number of species are present there will tend to be some degree of competition between them, and apart from this the struggle between the individuals of any one species will always continue. The point to be remembered is that it is this competition that must be the ultimate deciding factor in determining the actual range and abundance of any particular species.

It is very natural that the human conception of competition tends to be of an active physical struggle between plants of various kinds and between the individuals of a species, but a moment's consideration will show that by its very nature the plant (and particularly the land plant) is debarred from such active means of expressing itself. It is, therefore, of some interest to try and picture the way in which competition between plants may actually occur.

Perhaps the most obvious form of competition and the nearest to an active struggle is that between individuals, often in the seedling stage, for room in which to develop. It is, for instance, especially in this connection that we picture the "struggle for existence." Actually, of course, this form of competition is not restricted to seedlings and obtains between plants at all stages of growth, particularly perhaps at the stage of maturity, where the size and robustness of individuals must be of great importance. For instance, the growth-form of heather and other ericoids is such as to make difficult or impossible the presence of other plants where they grow. In such cases as these it is the physical contact or proximity of individuals which causes and controls the competition, and the question arises

whether this is the only form of competition and the only way in which plants can mutually affect one another.

The problems involved here have as yet received comparatively little attention, but there are many indications that this may be a very important and promising line of investigation.

It is probably fair to say that no one studies the detailed distribution of species and individuals over a limited area without being impressed by the way in which there is association between certain forms and dissociation between others. The whole arrangement of vegetation into edaphic types is based upon the facts of such association, and the question almost inevitably arises whether there may not be some factor or factors which favour close association between certain plants and preclude it between others. That is to say, whether there may not be certain factors inherent in certain plants which favour or inhibit the growth of others in close proximity. The actual edaphic requirements of plants must, of course, primarily control their presence in any particular spot, but as between two plants with similar edaphic needs the ultimate competition between them may sometimes perhaps be determined by factors inherent in the plants themselves.

This has been little studied so far, but it is significant that evidence is accumulating towards this point of view. Certain experiments, for instance (152, 153, 174), show more or less conclusively that if two species are grown together or in close proximity they may have a very considerable effect on one another.

Different pairs of species belonging to distinct genera or families have been grown together, and it has been found that with different combinations the relative growth of the components varies greatly. The hemp, *Cannabis sativa*, if grown with *Spinacia oleracea*, does very badly, while the spinach does very well. This is also the case, to a varying extent, when the spinach is replaced by *Secale cereale*, *Vicia sativa* or *Lepidium sativum*. On the contrary, the hemp does exceptionally well compared with its companion when the latter is *Beta vulgaris*, *Brassica oleracea*, *Lupinus luteus* or *Zea Mays*.

The same thing has been shown markedly in *Atropa Bella-donna*. When this plant is grown with *Sinapis alba* its growth is far below the normal, but if grown with *Artemisia vulgaris*, or particularly with *Galega officinalis*, its growth is appreciably above the normal. Again, when *Vitis vinifera* and *Euphorbia Cyparissias* are grown together in the same pots, the former's growth and especially its fructification is much lessened.

Another very interesting instance is that of the relation between the rye (*Secale cereale*) and *Viola tricolor*. Only in the presence of rye is it possible to obtain anything approaching a 100 per cent. germination of the *Viola*, and this is particularly significant because these two species may occur together naturally in the relation of crop and weed.

The suggested explanation of these facts is that many plants produce some sort of chemical emanation or secretion which is inimical to the development of certain other plants. These secretions are visualised as of three kinds, namely gaseous emanations from the aerial parts of the plant, as is well known in *Dictamnus*, and perhaps also in *Rhus Toxicodendron*; liquid or solid secretions from the leaves which tend to be washed down into the soil by rain (7); and secretions direct into the soil from the roots. It is the last which is presumably concerned in the cases mentioned above.

That at least something of the kind occurs is indicated by quite other observations, such as the intolerance of some plants to the presence of certain Crucifers,

and especially the mustards. Here there seems little doubt that some biochemical substance characteristic of these plants has some sort of toxic reaction towards other plants. Apart from the direct toxic effect of such secretions they may have a marked effect in determining the value of the habitat. It is well established, for instance, that acid or alkaline root secretions may seriously alter the hydrogen ion concentration of the soil water.

Still another observation bearing on the same point is that of the liberation into the soil of ethylene from organic sources (139).

However these results may be modified and their interpretations altered by further research, it seems reasonably clear at present that competition is to be regarded as something more complex than has been generally supposed in the past. Probably actual physical factors are the chief considerations involved and must almost of necessity be so normally, but there are at least indications that other factors and particularly chemical factors may play an important part.

It is also important to remember that the issue of competition may be decided at various stages in the life of the individual. For instance, the danger of overcrowding to species of large plants is usually marked only in the early and seedling stages, and once these have been passed the danger is generally over. Similarly the copious growth of ephemeral annuals may produce a temporary condition of danger which will pass in the course of a few weeks.

This rather lengthy discussion of competition may perhaps leave the reader with the impression that the relations between plants are naturally and always relations of antagonism. They may naturally be so but they are not always. One type of plant life may in fact provide the essential conditions necessary for the presence of another type or species, as is seen, for example, in plants which require to live in the shade of others as in woods or hedges, and in lianes and epiphytes. The continued growth of one species may also actually affect the substratum in such a way that it becomes colonisable by other species, as for instance in plants which inhabit the deep leaf-mould found in long-established beech woods. Sometimes the relationship is even closer, and this is particularly the case with parasitic or epiphytic plants whose ranges are determined by those of their hosts. Often quoted extreme examples of this are certain species of *Utricularia* which live exclusively in the water which accumulates at the base of the leaves of certain tropical American Bromeliaceae, and whose range is thus always correlated with that of the species they inhabit.

The conclusion therefore is that competition is itself but one aspect of a wider and more generalised factor of distribution, which is the influence of one kind of vegetation (or by analogy one kind of life, whether animal or plant) on the distribution of other plants. This general influence is often called the biotic factor, and at least in its aspect of competition must be regarded as of great importance.

This somewhat informal approach to the subject of the factors responsible for distribution has been made quite deliberately, in order to emphasise that these factors are only those that might be expected in the circumstances of the nature, life and history of the Flowering Plants. In order to arrive at what these factors are there is no necessity to possess any very profound botanical knowledge, because they will, to a large extent, become apparent in the course of such a discussion as has just been completed. It has, however, been rather lengthy, and we must now summarise the conclusions we have reached and go on to see how they compare with the conclusions reached on this matter by others.

In making this summary it is convenient to arrange the factors more in accordance with their mutual relations than was done above, where the main consideration was a cursive elucidation of them. When this is done, what has already been said may be restated in the form of the following table of factors concerned in the distribution of plants :

1. Place and time of origin.
2. Potentialities for dispersal.
3. Configuration of land and sea :
 - a. in the present.
 - b. in the past.
4. Distribution of climatic values (temperature, rainfall, light, wind) :
 - a. in the present.
 - b. in the past.
5. Distribution of edaphic values (physical, chemical, physiographic) :
 - a. in the present.
 - b. in the past.
6. Influences exerted by other plants :
 - a. direct competition.
 - b. indirect influences.
7. Human influences (not considered in detail).

These conclusions accord well with those of other authorities. Hayek, for instance (114), recognises :

1. Climatic factors ;
i.e. light, temperature, atmospheric pressure, precipitation and wind.
2. Edaphic factors ;
i.e. soil.
3. Biotic factors ;
i.e. influence of the animal world, influence of man.

Thomson (172), comprehending the distribution of both plants and animals, arranges the factors in three pairs thus :

- a. The physical peculiarities of the region under discussion, and the constitutional peculiarities of the living creatures.
- b. The original headquarters of the stock (usually uncertain), and the means of dispersal in each case.
- c. The physical changes of climate, earth-movements, etc., in the region, and the changes brought about in the struggle for existence between the various living tenants of the country.

Both these authorities point out that there are also many minor additional factors, and also that those mentioned interact so as to produce a very complex state of affairs.

Du Rietz (65) gives a rather more elaborate classification, especially in regard to biotic factors, which is of interest as incorporating the essential factor of time, not mentioned in the above two schemes, namely :

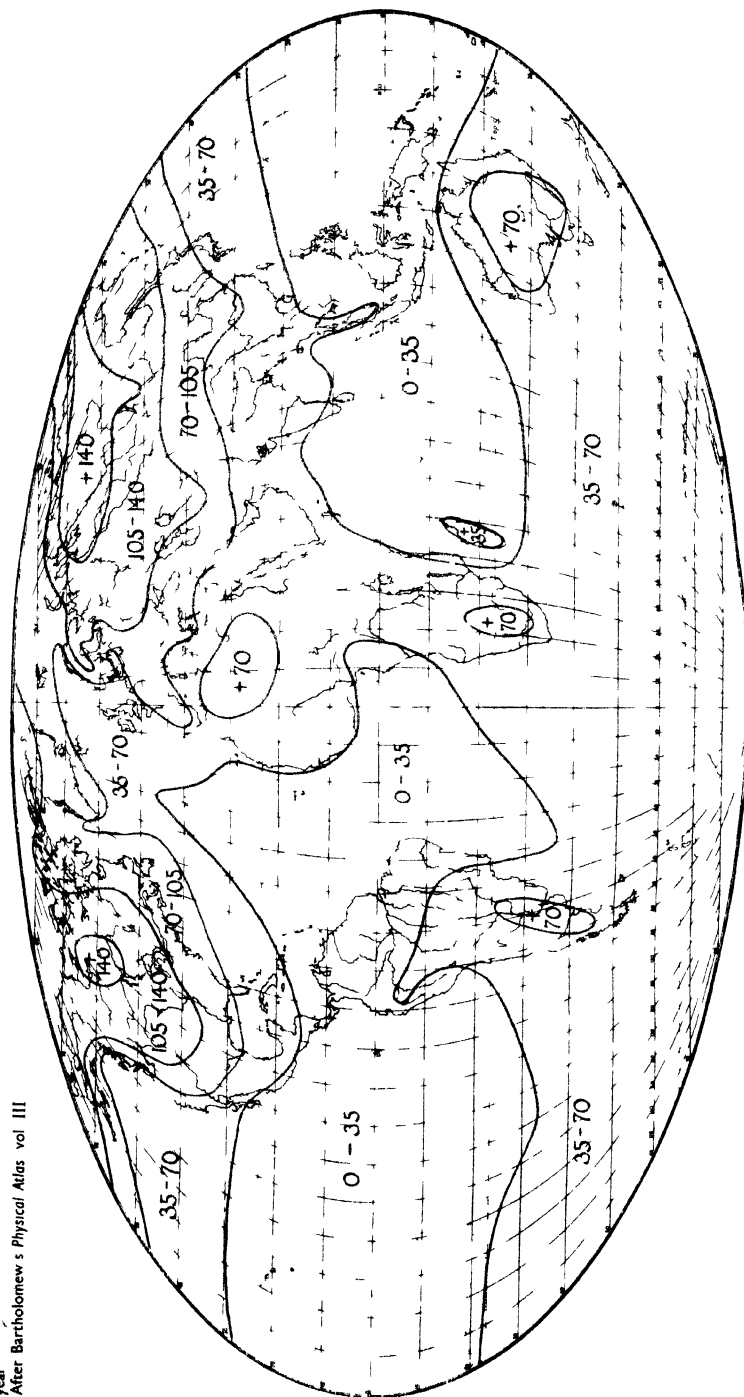
A. Actual factors—

I. Abiotic :

- a. climatic.
- b. edaphic.

Map of the World showing, in degrees Fahrenheit the range of extreme temperature variation during the year
 After Bartholomew's Physical Atlas vol III

PLATE 21



Areas correct Distortion increasing towards border of map
 Approximate Scale 1:100,000,000 1 inch = 1600 miles
 on Mollweide's Homographic Projection
 C. 1917

II. Biotic:

a. non-anthropogenic—not influenced by man—

1. phytobiotic:

a. climatic—such as shadow, wind, shelter, etc.

b. edaphic—such as humus, soil, humidity, etc.

c. pyric—effects of fire.

2. zoobiotic—presence of excreta, carcasses, etc.

b. anthropogenic—due to man's influence—

1. direct.

2. indirect.

B. Historical factors (with all the same groups as “ actual ”).

He also gives a classification in which he sets out the factors influencing “ the distribution of species upon a certain spot during a certain period.” They are six in number, namely:

1. Nature of habitat at beginning of period.
2. Distribution of species upon or near the spot at the beginning of the time factor.
3. Supply of dispersal units.
4. Strength of each species in competition.
5. Interference of animals, man, and plant parasites.
6. Time elapsed.

Here there is recognised as a separate edaphic factor an effect which has not previously been specifically mentioned, namely fire. Fire may often be due to human action, but in certain parts of the world it is a normal occurrence at certain seasons, and in response to it certain peculiar features of the vegetation in these regions have been developed. The subject will be dealt with more fully later.

These specimen classifications of factors show two things—that the differences between them are mainly due to a difference of opinion as to what may justifiably be termed a factor, and that the arrangement arrived at above incorporates, within the limits of its detail, all the relative types of factors. It does not, however, mention all the aspects of these factors, and we must therefore pass on now to a more detailed and factual account of those factors which have not already been sufficiently discussed, or which are susceptible to further treatment. These are dispersal, climatic factors present and past, edaphic factors present and past, the configuration of land and sea present and past, and certain aspects of the mutual influences of plants.

Before doing this, however, there is one more subject to be mentioned. This is the migration of species or of floras, and it is rather a consequence of the interaction of the factors outlined above than a factor itself.

It cannot be doubted that if the factors which have been described have all played a part in controlling plant distribution—and it is the purpose of the next few chapters to demonstrate this—plant distribution must be regarded as something in more or less constant flux and rarely if ever constant for more than a short period. The fluctuation may be visualised as of two kinds, first in respect of the floristic constitution of any flora, and secondly in respect of the position of various floras.

That the latter and more important type of change has taken place is demonstrated wherever there is evidence that a particular area has been occupied at successive periods by different assemblages of plants. Unless it can be assumed that each successive flora developed *in situ*, it must be believed that the later ones in turn displaced those that went before, and such an assumption being out of the

question, if on no further grounds than those of time, this belief is justified. Again, if an earlier flora is found at a later date in a different position and contemporary with the flora which replaced it in its original site, we may assume that very extensive movements of floras over the surface of the world must have occurred.

The evidence of migration is thus chiefly palaeobotanical, and it is very copious and unmistakable. There are repeated examples of superposed floras of different types, as well as of similar floras changing position with the passage of time.

We need not go beyond the bounds of Great Britain to demonstrate this and to see how even one small country has been the home of a succession of floras one after the other. Almost every geological horizon has revealed a different type and constitution of native flora.

Particularly is migration revealed in the special geological matter of glaciation, and we need only remind readers of the later history of the British flora and particularly of the changes which have taken place between the earlier Pliocene and the present day. At the former time the flora was much as we know it now, but in the interim much of it was undoubtedly forced out of the country, to return once more at a later stage. In North America the degree and extent of the floral movement were almost certainly even greater.

In this particular instance of the effect of glaciation it is fairly certain that the result of the climatic change was to telescope up the floristic and climatic zones rather than to eliminate the higher values, and the lowlands of the equator do not seem to have been appreciably colder than they are now. At the same time the spread of the ice must have diminished the total area open to plant growth very considerably. In these circumstances it is impossible to deny the probability not only of floral migration but also of increased floral mixing, and so these same geological evidences afford examples of the first kind of fluctuation mentioned above, that of the constitution of different floras.

But this kind of migration, the movement by which independently originating floras become mixed so as to consist of or show elements derived from various directions, is shown even better and more generally in the present world flora. Perhaps nowhere in the world to-day can it be said that the flora consists entirely of plants which have originated locally. Almost always the flora contains some proportion of foreign ingredients. Clearly there must be some kind of differential movements of floras to produce this effect—there must be an infiltration of forms from the frontiers or from distant lands, and where, as in many cases, this infiltration seems to have taken place from many directions, its effect is even more striking.

The same thing is seen in the difficulty which exists in defining certain floristic areas or regions, and a brief reference back to Chapter 2 is sufficient to show how real this sometimes is, and how in one or two cases the word transitional has even been used to describe certain regions. The difficulty arises simply because these particular parts of the world's surface have become focal points at which streams of migration or infiltration from various directions meet. The largest of these is undoubtedly in eastern Malaya, where there is a most conspicuous mixture of Asiatic and Australian floras, and the problem of just where the line of demarcation between the two is to be drawn has puzzled many investigators. The fact of the matter is that in passing from Asia to Australia the change in floral constitution as between Asiatic and Australasian plants is so gradual and the mixing so complete that it can hardly be disentangled.

Similarly, but on a lesser scale, the more southerly parts of the East African coastal belt are a notorious transition region where the northern parts of the

South African flora and the southern parts of the tropical flora have met and mingled (24).

The flora of the high alpine region at the junction of Tibet, China, Burma and India is another very marked instance, and the flora of this general region contains elements of the flora of each of the neighbouring countries, a fact that is reflected in the degree to which the flora as a whole can be divided in geographical detail.

Migration and mingling of this kind is perhaps least seen in America, and the presumptive reason for this is interesting. When two moving societies begin to mix in the way that has been indicated it is only a matter of time before the mixing is complete, and the result is a homogeneous one with, as time goes on, an increasing character of its own. Hence where this mixing is most conspicuous and localised, as in the instances given above, it is reasonable to suppose that it has not been going on very long. This, of course, will depend on the length of the opportunity for such mixing. In America the indications are that there have been opportunities for the mingling of at least most of the floral elements of the continent for a very long time, and indeed that such prolonged mingling has been in progress. As a result it is far less in evidence than in the Old World.

In the last paragraphs infiltrating migration has been pictured rather as something resulting from two reciprocal and equal actions. This appears to be by no means always the case, and sometimes the movement has been largely or almost entirely in one direction. Perhaps the best example of this is the spread of plants along the north-south mountain ranges of the world, as, for example, down the Andes or through Malaya. In these cases there seems to have been little or no counter-movement.

In terms of the present world flora it is perhaps not too much to say that floristic mingling caused by this kind of migration is one of its most general features, but, whether this is a fair statement or not, the instances which have been mentioned in conjunction with the geological instances of wider migration are ample to show that actual movements of assemblies of plant species over the world in various directions have taken place as a more or less direct consequence of the distributional factors outlined above.

CHAPTER 16

THE FACTORS OF DISTRIBUTION—II. CLIMATIC FACTORS

CLIMATE may be described as the physical state of the atmosphere and may be regarded as the result of the sun's influence on the layer of gases that covers the surface of the earth. This total physical state of the atmosphere is composed of a number of different constituents which it is convenient to term the elements of climate. Of these temperature and moisture are the most important, but there are a number of others of secondary significance. Most of these do not call for any extensive treatment in this chapter and it will be sufficient for our immediate purpose if climate is regarded as consisting essentially of four aspects, temperature, precipitation, light and wind. It would be difficult to maintain that this is invariably their order of importance, but, as will be seen, it represents their general relation and it is convenient to deal with them accordingly.

The problem of the influence of climatic factors on plant geography has been discussed by many writers and it is not possible to refer here to all the important sources of information on the subject, but the reader will find much of interest in publications by Livingston and Shreve (149) and by Zotov (271).

Temperature

(Plates 20, 21)

It is believed that the interior heat of the earth, although considerable, contributes but negligibly to the heat of the atmosphere, which is derived almost entirely from the sun. At the same time it must be remembered that the heat of the atmosphere is not the only direction in which temperature affects plants, and that the heat of the soil, which is itself derived from the heat of the atmosphere, has also an important influence. For our present purposes, however, the latter may be regarded as generally proportional to and determined by the former.

The basic consideration determining the distribution of temperature in the earth is the shape of the globe, and its inclination to the direction of light and heat coming from the sun. In equatorial regions the incident rays from the sun not only reach the earth almost perpendicularly but thereby pass most directly through the atmosphere. Progressively away from the equatorial regions the curvature of the earth not only causes the incident rays to strike more and more obliquely but also causes them to pass less directly through the atmosphere, until at the poles they may be said to be almost parallel with the earth's surface.

For these reasons the basic distribution of temperature value is a latitudinal one showing a gradual and considerable diminution between the equator and the poles (see Plate 20). At the same time the precession of the equinoxes causes the gradients in both northern and southern hemispheres to vary with the seasons, so that they are least steep in the summer and most steep in the winter. The latitudinal zonation of temperature must therefore be regarded as in a state of regular oscillation.

Since the two main factors of the position of the sun and the thickness of the atmosphere are to all intents and purposes constant, it might be expected that the latitudinal distribution of temperature would be perfectly regular and symmetrical on both sides of the equator. There is no reason to suppose that this would not indeed be the case were the surface of the earth exactly the same in all places—if, for instance, the surface were entirely land and that land were of constant height. As it is, neither of these states prevails. The distribution of land and sea is very complex and irregular, and in addition the relief of the land is extremely varied.

Both these features influence temperature to a considerable extent. The general effect of large areas of sea is to tone it down and to reduce extremes, and it may also have a secondary effect through the influence of warm or cold currents. Elevation of the land has the general effect of reducing the normal latitudinal values of temperature.

It may be expected, therefore, that the actual distribution of temperature will be a latitudinal one modified by these two considerations, and a glance at a temperature map of the world will show that this is indeed the case. As a result the world can be divided into a series of rather irregular latitudinal zones on the basis of temperature, as is, of course, perfectly familiar in such terms as “tropical,” “temperate” and “arctic,” the irregularity depending on the degree of variation in the distribution of land and sea and of altitude. In this distribution the equatorial values tend to remain more or less constant throughout the year, but elsewhere they oscillate between maxima and minima according to the season, the hemispheres alternating in this respect.

These circumstances lead, on the land surfaces of the earth, to the occurrence of two rather distinct types of climate based chiefly on their temperature features. Away from the influence of the sea, that is to say towards the interior of the larger land masses, the climate is “continental” and characterised by comparative extremes of heat in summer and of cold in winter. On the edges of large land masses and on islands there is an “oceanic” climate characterised by more moderate variation and less extreme seasonal values.

The effect of altitude is much less generalised and more localised, in accordance with the irregular distribution of elevated regions. It is true that a great part of the world’s land surface is raised considerably above mean sea level and that therefore the temperature values tend to be widely modified, but it is only in the regions of excessive elevation in the more temperate latitudes that the modification becomes strikingly apparent. Especially is it noteworthy in the huge plateau system stretching north from the Himalayas, and on a smaller scale in the areas occupied by the great mountain systems of western America, but it is seen to some extent in practically all the mountains of the world.

Ocean currents, by bringing either colder water into warmer seas, or *vice versa*, tend to effect the distribution of temperature wherever they occur except when their direction is latitudinal, but in fact there are only two regions of the world where the effect on a world-wide scale is marked. These are in the north Atlantic and north Pacific oceans, where the Florida and Gulf Streams and the Kuro Siwo current respectively cause the isotherms to deviate far to the north by the influence of the warm waters which they bring from the tropics.

The main features in the distribution of temperature are shown in Plates 20 and 21, but they may conveniently be summarised here. Annual isotherms, that is lines of equal mean annual temperature, are basically latitudinal, but they

are distorted northwards by warm ocean currents in the northern hemisphere and southwards on the land masses of the southern tropics.

The average minimum temperature varies from -76° F. in north-east Siberia to over 68° F. in Guiana and most of Malaya. It is below -40° F. in much of northern Canada and Siberia.

The average maximum temperature varies from below 68° F. in parts of North America and north Asia to over 113° F. in parts of the south-west U.S.A., in the African-Indian desert, and in parts of Australia, and is above 104° F. over a considerably wider area.

The annual mean range of temperature varies from under 10° F. in most of the tropics to over 120° F. in part of Siberia.

The annual extreme range of temperature varies from about 20° F. in parts of the tropics to 170° F. in parts of north-east Siberia.

Constancy of temperature throughout the year is very important in plant distribution and is perhaps to be regarded as the essential character of climate in the tropics.

A last general point about the distribution of temperature, and indeed of other factors too, is to remind readers once more that the northern hemisphere is a land hemisphere and the southern a water hemisphere, so that great caution must be used in comparing conditions and values in the two.

The correlation between plant distribution and climate is shown more clearly in the case of temperature than anywhere else, and indeed is so obvious that it scarcely needs demonstrating, as our common application of such words as "tropical," "temperate," "hardy," "tender" to plants shows. It is here, however, important to draw the proper distinction between flora and vegetation, because it is especially in the limitation of the range of species and other units that temperature is important. It has already been seen how few plants are anything like cosmopolitan in range, and what a marked distinction there is between tropical and temperate forms. Indeed, it is fairly true to say that the reason why there are not more completely distributed plants is that most wide species are ultimately limited by considerations of temperature.

This is to be seen almost everywhere. Our own flora affords many instances in which species occupy the more southerly part of the country but do not range far north. Similarly with the question of casuals: the factor which prevents them from establishing themselves is temperature—not, it will be noticed, temperature at all times, or they would clearly not occur at all in the country, but temperature at some season of the year.

The way in which temperature acts as a limiting factor of distribution seems to be twofold. In the first place a low temperature may not provide that combination of heat quantity and quality which is necessary for the production of seed and fruit, as is the case with the casuals just mentioned, but there is generally also a temperature minimum below which even the vegetative life of the plant cannot continue.

This will actually determine whether a species can occur in a given area, and clearly the higher the temperature needed for growth the narrower will the potential area of the species be. It would seem, however, that most plants can live vegetatively over a fairly wide range of temperature provided that this does not fall below freezing point. This is not to say that they can reproduce, but they can exist, and this is shown by the innumerable examples of garden plants from warmer countries which are hardy in this country except in very extreme conditions.

The question of frost raises quite a different problem, because it involves the possible injury of tissues by the expansion of their juices when they freeze. It is significant that there are no flowering plants which pass the whole of their life history in a temperature below freezing, and there is probably none capable of doing so. Indeed, very few can survive serious freezing during the time that they are in full vegetative vigour. Naturally the lower the temperature the greater its effect is likely to be, but there is reason to suppose that very often the duration of freezing is more important than the actual degree of coldness, and Shreve (218) has shown this to be the case with certain cacti, one of which (*Opuntia missouriensis*) successfully resisted 375 continuous hours of frost, while others were destroyed by much shorter periods at the same temperature.

Plants which inhabit regions where frost is general during the winter season normally spend that period of the year in some condition which protects them from the dangers of freezing. This process of self-protection against winter rigours is called perennation and is carried out in a variety of methods such as the restriction of life to buried organs only, the loss of leaves during autumn, and so on. The winter may also be passed in the seed condition, where the plant is not only dormant but protected by various resistant structures.

This indeed seems to be the normal process in ephemeral annuals. Some seeds may germinate in the autumn and endeavour to pass the winter as young seedlings, and may, if the conditions are not too bad, succeed in doing so, but there are always many seeds which do not germinate till the following spring, when it may be presumed safe to do so.

It is in relation to temperature as a geographical factor that the subject of growth-forms is most appropriately mentioned. It has long been recognised that plants can be classified according to their general form, and many people have published such schemes, but the study of growth-forms is especially associated with the Danish botanist Raunkiaer (192). He recognises the following main forms, each of which is further classified in detail. The names used are for the most part indicative of the chief features of the types.

- | | |
|------------------------|---|
| Phanerophytes . . . | Plants whose size is not appreciably diminished in cold or dry seasons. It includes all woody perennials of erect habit and also many epiphytes and succulents. At least a dozen minor types can be recognised. |
| Chamaephytes . . . | Subshrubs or herbs which partially die back in winter or which grow closely adpressed to the surface of the soil. This includes cushion plants. |
| Hemicryptophytes . . . | Plants which lose practically all their aerial parts in winter and are visible above the surface only as rosettes or offsets. |
| Cryptophytes . . . | Plants which disappear entirely to below ground or water during winter and which perennate by rhizomes, bulbs and corms, or by under-water buds. |
| Therophytes . . . | Plants which pass the winter in the seed, as most annuals. |

This classification might be paraphrased as one which is based on the degree to which plants find it necessary to protect themselves against winter conditions. In these terms the phanerophytes include the plants which are under no such necessity, as well as those in which the method is least obvious. In the other groups the degree of protection, which is usually the reverse of exposure, becomes

progressively more marked until it culminates in perennation in seed form, which may be regarded as the last resource.

One slight complication needs to be explained here. In some parts of the tropics, where temperature conditions are always more or less at an optimum, growth continues all the year round, but in other parts there is an unfavourable period due to an uneven distribution of rainfall in time. In other words, here the winter cold unfavourable season is replaced by a dry season where the danger is desiccation instead of refrigeration. This point will be returned to later, but it is worth noting here that the two distinct dangers are met by plants in much the same way.

As to the absolute temperature values which flowering plants can stand, two general statements seem to be true: first, that little or no development goes on at temperatures below freezing; and second, that there are no parts of the world where the temperature is too high for growth and reproduction. As will be seen, there are regions where the plant life is very scanty, and some where it is virtually absent, but this is not due solely to temperature values.

The relation between plant distribution and temperature alone is perhaps most clearly seen in the case of aquatic plants, and especially in the marine Angiosperms, because here many of the complicating related factors such as other air conditions, precipitation and so on are absent. Plants living in the sea may, it is true, be affected by the chemical constitution of the water and also by the movement of the water in the form of currents, but the former is reasonably constant and the latter does not seem to be a decisive factor in the determination of range, and it is fairly safe to say that the one really important consideration must be temperature. With this belief the account of the distribution of Angiosperms in the sea as illustrated by Plate 15 is very significant. Above all, the occurrence of prevalent latitudinal distribution limits will be noticed, and it can scarcely be doubted that these are due to the temperature relation of the species concerned. Moreover, it is clear that this relation must be a very exact one, because the latitudinal temperature gradient in the sea is very gradual.

The importance of the modification of the general latitudinal distribution of temperature by elevation as a factor in distribution can scarcely be overestimated. In rising vertically above the mean sea level there is a fall of temperature of approximately 3° F. for every 1,000 feet, so that all mountains reproduce, according to their height, a temperature range corresponding to that between certain latitudes at sea level, and any mountain which has permanent ice and snow epitomises the whole temperature gamut at sea levels between the latitude in which it is situated and the nearer pole (fig. 1). Thus a mountain on the equator which is high enough to have permanent snow reproduces on its slopes the temperature gradient of a whole hemisphere.

For this reason mountains provide habitats, as far as temperature goes, for plants characteristic of quite different latitudes, and thus afford a series of stepping stones in range which is often of the greatest value. It has been seen that many plants occur in the temperate regions of both hemispheres, and are therefore to be regarded as having crossed the tropics in the course of their spread. This they have certainly done by way of mountains, which, for the reason mentioned, afford a pathway for their movement.

It is often not sufficiently realised how widely distributed in the tropics are mountains of great elevation, but actually they are of common occurrence. Most obvious is the great range of the Andes, which, while indeed of least magnitude in

the north parts of the tropical zone, does in fact provide a more or less continuous line of peaks between north and south.

Less noticeable, but none the less serviceable, are the mountains which stretch in an almost unbroken line from the Himalayas down the Malay Peninsula and through Malaya to New Guinea, whence the step to Australia, which has itself an elevated eastern border, is short.

Only in Africa is the situation rather different, not only because there the heights are less continuous but because a particularly wide break of desert regions cuts them off from the northern temperate mountains of Europe. Also at present at least there is enormous oceanic discontinuity south of Africa.

In view of these facts the occurrence of bipolar plant types is almost certainly due to the fact that they have succeeded in crossing the tropics by passing along mountain chains, and this they have been able to do because of the peculiar temperature relations which the mountains afford.

Incidentally it may be added that Du Rietz (66) and others have shown that some species have probably crossed the tropics by the New World mountains, some by the Malayan route and some by both means.

This view is supported too by the present occurrence on nearly all tropical mountains of types which are either identical with or very closely resemble those of the temperate regions and especially those of the north. Allusion has already been made to northern genera with extensions into the tropics along the mountains, and this is specially notable in America, though only less so in Malaya. Van Steenis (249) has made a careful study of the mountain flora of Malaya and has shown how many northern forms there are in it, and also the routes by which they apparently came.

In Africa too the same is true, except that here, owing to the peculiar distribution of the mountains, the relationship with the north is more discontinuous. Time and again, however, the prevalence of northern types on the African mountains has received comment, and indeed many of our familiar British plants occur there, as, for instance, *Sanicula europaea* and *Epilobium hirsutum*, while many years ago *Linnaea borealis* was reported apparently growing wild on the slopes of Ruwenzori.

Precipitation

(Plates 23, 24)

Under this term are included all forms of atmospheric moisture, but it will simplify the discussion if we consider it in terms of rainfall only, remembering nevertheless that such other forms as snow and dew are sometimes of great importance.

The distribution of rainfall is essentially different from that of climate in that it is not regularly latitudinal. It is true that the heaviest rainfall tends to be in parts of the equatorial or at least tropical zone, but the main feature of its distribution is that nearly all values tend to occur in nearly every latitude. This alone is sufficient to show, bearing in mind the general distribution of plant life already described, that of the climatic factors rainfall is to be regarded as secondary in effect to temperature.

It is particularly with the relative importance of heat and rainfall that we can illustrate the difference between floristic and vegetational distribution. It has

been seen that floristic distribution, that is to say the distribution of taxonomic units, is predominantly a latitudinal one. The distribution of vegetation types, on the other hand, is predominantly one of precipitation. That is to say, such vegetation types as forest and grassland tend to occur at any latitude in certain rainfall values, while deserts are similarly distributed where rainfall is inadequate. To put the matter from a rather different point of view, it may be said that in matters of plant geography temperature is more fundamental than rain; in matters of plant ecology, in the sense of vegetational development, rain is more important than heat.

Owing to the absence of any basic latitudinal zonation, rainfall, even more than temperature, is correlated with the distribution and relief of land and sea. This is because winds coming from the sea will be moisture-laden, and also because elevated regions may protect inland areas from the influence of these winds. Rainfall must therefore be considered as very directly related to wind, and reference should be made to the discussion of that subject below.

As it is, the simplified distribution of rainfall is roughly as follows. Regions of maximum rainfall are nearly all equatorial, namely the lowlands of Brazil, parts of west Africa, and the whole of Malaya and the Pacific. In all these the total annual rainfall is above 80 inches. Other more localised regions with similar values are the east coast of Brazil, parts of the west coast of South America, the east coast of Madagascar, the Himalayas and Burma, parts of south India, New Zealand and a small area in Alaska. The highest annual figures recorded (about 450 inches) are from single stations in Burma and the Hawaiian islands.

Regions of exceptionally low rainfall, under 10 inches a year, are in the arctic, parts of western North America, parts of temperate South America, North Africa and Arabia, Central Asia, South Africa and the interior of Australia. Elsewhere the distribution of rain varies from 10 to 80 inches annually.

The two main features are undoubtedly the practically continuous area of excessive rainfall from the Himalayas through Malaya and far across the Pacific, and the almost continuous range of low rainfall, leading to desert conditions, which stretches from the west coast of North Africa practically to China.

The general correlation of species distribution with this distribution of rainfall will be apparent from the close correspondence of some of the floristic regions with it, but reference to total annual rainfall is not enough to show this correlation fully.

Obviously the absolute amount of rainfall must be of primary import, but except where this is definitely inadequate a much more significant aspect is the distribution of the rain during the year, that is to say during the various phases of the plant life.

In brief the following conditions are to be found:

1. Heavy rainfall all the year round.
2. Moderate rainfall always, becoming heavy at certain times.
3. Moderate rainfall throughout the year.
4. Moderate rainfall concentrated in the summer.
5. Moderate rainfall concentrated in winter.
6. Low rainfall spread over the whole year.
7. Low rainfall concentrated in one season.
8. Relative absence of rain.

A rather different classification, of which Plate 24 is a somewhat simplified edition, recognises six types, as follows :

1. Constant drought :
N. Africa to India, C. Asia, California, western S. America, S. Africa and C. Australia.
2. Periodic rains :
 - a. summer rain, dry winter and spring—
especially in the monsoon regions of Asia, western Africa and parts of tropical America.
 - b. winter rain, summers dry—
Mediterranean, western N. America, Cape, western S. America and S.W. Australia.
3. Rain at all seasons :
 - a. maximum in summer—
tropical S. America, eastern N. America, Europe and W. Asia, parts of Malaya.
 - b. maximum in winter and autumn—
W. Europe, parts of Malaya, N. Pacific coasts, Fuegia, and New Zealand.
4. Continuous rain, no month with less than fifteen rainy days :
occurs only in parts of certain oceans.

Light

As Hayek (114) and others have pointed out, light must, in one sense at any rate, be the fundamental climatic factor in relation to plants, because the chemical process, photosynthesis, which is the basis of the whole of their physiology, is, as its name implies, one which goes on only in the presence of light, so that in its absence plant life as we know it to-day could not continue.

This is, of course, perfectly true, but our concern here is rather with the effects of various climatic factors in limiting the actual distribution of plants, and in this respect light is of comparatively minor importance.

Owing to the shape of the earth the insolation of the equatorial regions is stronger or at least more direct than that of the latitudes further south and north, but there are no data to indicate that tropical plants require stronger light than temperate ones. On the other hand, many plants protect themselves from extreme insolation by some structural or chemical means. Nor is the value of insolation at any spot always constant. It may be greatly modified by the degree of cloudiness, and this being so, it may be assumed that ordinary sunlight provides appreciably more light than plants actually require, and that nowhere, during summer months at least, is it deficient.

The main effect in the distribution of light values seems, on the other hand, to be the length of time of illumination. In the equatorial regions the day is about the same moderate length all the year round, but towards the poles the day becomes longer in the growing season and shorter in the winter, until in the arctic and antarctic there is more or less continuous light for six months and a corresponding length of darkness.

Much experiment has been done on the effect of length of day on plants, and it is becoming generally recognised that plants tend to be either short-day plants or long-day plants, the former being in general the tropical species. In temperate lands the short winter day does not affect the question, because the plant is dormant during this period of the year.

It is doubtful whether this distribution of length of day is to be regarded as a distributional factor. Rather it would seem that species which are latitudinally limited for other reasons become adapted as it were to the length of day in their ranges.

Wind

Broadly speaking, wind, that is to say air in motion, is the result of local variations in the pressure of the atmosphere, and we must therefore, in discussing the effect of wind on the distribution of plants, keep in mind its relation to barometric pressure. This latter alone, however, has not received much attention as a direct factor nor does it appear to be important as such, though it has been suggested that there may be optimum pressures for certain plants.

Wind may be regarded as of potential effect in plant geography in three ways These are:

1. By its physical influence on the growth-form of plants, as in restricting or preventing the growth of trees. In the Falkland Islands, for instance, wind seems to have exerted a considerable influence on the nature of the vegetation in this way.

2. By its effect on dispersal. Here a distinction must be drawn between land winds and oceanic winds. The latter have a fairly simple distribution, but the former are very complex and variable, depending on all sorts of extraneous factors, and, although there are prevailing winds, it is probably true to say that in most land areas wind direction varies greatly. This is obviously of great potential significance in dispersal, which normally occurs only at certain seasons of the year.

3. By its effect in determining other climatic values. Two climatic elements are especially liable to be varied by wind, namely temperature—which becomes lowered by the increased evaporation that results—and rainfall. Indirectly the absolute amount of this latter may be affected, but wind chiefly controls it by determining its direction and the areas over which it will fall. The North-east Monsoon is perhaps the best example of this.

As has been indicated, it is almost impossible concisely to describe the normal distribution of wind over the continents, but the general planetary circulation of the atmosphere, particularly over the oceans, is fairly simple. Extending for some distance on both sides of the equator is a belt, the doldrums, where the pressure is low and winds are very light. North and south of the doldrums are the two great belts of the trade winds, strong steady winds blowing, in the northern hemisphere, from the north-east, and, in the southern hemisphere, from the south-west. Between the latitudes 30° and 40° are the northern and southern horse latitudes, which are regions of high pressure and comparative calm. Between the horse latitudes and the poles are the westerlies, strong winds predominantly from the south-west and from the north-west respectively in the northern and southern hemispheres.

Bush Fires

Apart from their direct effects upon the distribution of plants, climatic factors often exert their influence in indirect ways, and as one striking example of many such the case of bush fires may appropriately be mentioned.

The deliberate and periodic burning of vegetation is a feature of many systems of agriculture, especially in the tropics, but in certain parts of the world the combined features of climate and vegetation are such that seasonal fires are a normal and

natural occurrence. This is true, for instance, in parts of the savannah zones of tropical Africa, where there is a prolonged dry season. How these fires start is not altogether apparent, but both lightning and incandescent volcanic materials are known to be amongst the causes (204).

In Angola, where the vegetation is a patchwork of dry forest and grassland, the latter is regularly burnt during the dry season. Associated with the grasses are many perennial plants, and these are characterised by exceptionally well developed and peculiar underground rhizome systems by which they are able to survive even when their aerial parts are burnt. Equipped thus such plants are therefore able to exist where others would almost certainly be destroyed. Exell (75) gives, as good examples of these fire-resisting plants, species of *Tetracera*, *Combretum*, *Annona*, *Eriosema*, *Geissaspis*, *Aeschynomene* and various Rubiaceae.

Climatic Regions

It is evident from what has been said in the foregoing pages that the surface of the earth can be classified into regions or areas according to the values of any one of the climatic elements that have been mentioned. But it is possible to go further than this and to divide the world up into what may be called general climatic regions with regard to which all the major climatic elements and values are taken into account.

This has been done by a number of geographers, and as an illustration of their results the system proposed by Supan, in which the world is divided into thirty-four climatic provinces, has been used as the basis for Plate 5. The names of the various regions are more conveniently given with the plate and need not be repeated here, but the main purpose of the plate may well be emphasised once more. It is to demonstrate, by comparison with Plates 2 and 4, the remarkable degree of similarity existing between the general distribution of floras, of vegetation, and of climate. These three maps, in particular, show more graphically than any words can describe the close correlation between plants and climate, and the truth of the statement that climatic factors are among the most important of all the forces controlling plant distribution.

CHAPTER 17

THE FACTORS OF DISTRIBUTION—III. EDAPHIC FACTORS

In Chapter 15 it was shown that the ordinary flowering plant is living in contact with its environment in two directions, its aerial parts being surrounded by the air and the subterranean parts by the soil, and that environmental factors may therefore be divided into climatic and edaphic. The former have been discussed: the latter are the subject of this chapter.

As regards the Flowering Plants it may be said that some amount of soil is a primary necessity for the growth of plants and that none can live on the bare surface of rock.

Soil may be described as the products of the disintegration of rocks, both sedimentary and igneous, by the process and effects of weathering, that is to say by the action of various climatic influences. To take but one of the more conspicuous instances, frost is a very potent rock breaker. All but the hardest rocks tend to become more or less soaked in times of rain; this contained water expands when it freezes and in doing so splits the rock in varying degree. The mere physical action of prolonged rain too will in time wear away even the hardest rocks.

As a result of this weathering the surface layers of rocks become sooner or later broken up so that three distinct layers can be recognised. Actually on the surface where the effects of weathering are greatest there is a thickness of soil proper where the rock has become more or less completely disintegrated. Below this for a varying thickness is the subsoil, where the weathering has begun the process of breaking up the rock but has not taken it very far. Below this again is the solid rock itself unchanged.

The physiological processes of the plant are such that it can make little use of and take little from disintegrated rock unless the process of disintegration has proceeded to a very considerable extent, and hence its soil relations are almost entirely those of the actual soil layer, although to varying degrees the subsoil may be of importance.

In the normal course of events weathering will result in the development of soil *in situ*, that is to say immediately over the rocks from which it is derived, and such soils are called local soils. On the other hand, circumstances will sometimes result in the washing away or other transportation of the soil from its point of formation, and its subsequent deposition elsewhere. Such soils are called transported soils. The main influences producing them are wind action, such as causes the accumulation of blown sand; glacial action and the movements of glaciers, as is illustrated by boulder clays and other morainic deposits; and rain and river action such as can be observed in any delta. It is worth noting that all three are capable of producing areas of soil where there would otherwise be water, and especially of producing bare soil areas open to plant colonisation. For instance, much of Holderness, in Yorkshire, would be beneath the surface of the sea were it not for vast accumulations of boulder clay and other glacial deposits. Similarly

in tidal rivers fresh surfaces of alluvium are constantly being formed and may become permanent. In the case of both tidal mud and sand-dunes, however, subsequent action often tends to remove and redistribute accumulations of this kind.

The rooting of plants in soil has a twofold function. Chiefly it enables the plant to absorb such food materials as it requires from the soil, but in addition to this it serves as an anchorage and provides the base upon or from which the aerial parts may grow up into the atmosphere. Generally speaking, the larger the plant the firmer and deeper the anchorage it will require, and so the absolute amount or depth of soil is a primary factor, in the sense that no plants can flourish unless there is a sufficiency of soil for the proper development of their underground parts.

Another very important point about soils in general is that the continued growth of plants in them tends to add greatly to their depth and bulk. Generation after generation plants grow and die and the products of their decay are washed down into the soil, and in certain circumstances the upper layers of the earth's surface may indeed come to be composed of little else than organic matter. This organic constituent of the soil is known as humus and is sometimes very conspicuous, as in the deep layers of leaf-mould in beech woods and in peat. On very hard rocks it sometimes happens that the growth of flowering plants is only possible by reason of this accumulation of humus, and it is one of the great dangers of fire that its effect is not only to destroy living plants but also to destroy much of the soil in which they might live. This is particularly serious in that the soil so lost cannot quickly be replaced, and the whole immensely long development of the accumulation of a humus soil has to be gone through again before large plants can become established. This occurs, for instance, in parts of Canada where the underlying rock is very hard.

Except in new soils there will always tend to be some proportion of humus, and this constituent is of the greatest importance not only for the substratum it may provide but in determining the characteristics of the soil as a whole. Newly deposited transported soils are often exceedingly poor in many of the more necessary minerals and may contain no humus at all, so that their rapid colonisation by flowering plants is sometimes difficult to understand. New sand-dunes in this country, for instance, are often colonised almost from their inception by at least one Angiosperm, though analysis may show them to be composed of silica and carbonate of lime without measurable quantities of anything else. Yet in this apparently inhospitable medium *Ammophila* will flourish, and is soon joined by other species.

This outline of the methods by which soils are formed is sufficient to indicate the general differences which will be found between them. The most obvious and direct of these are in physical and chemical constitution, but to these must be added a biotic factor depending upon the living inhabitants of the soil, and to-day there is a growing appreciation of the importance of this factor.

The physical condition of the soil depends on four considerations, all of which are more or less intimately related to climatic conditions. First is the question of depth, which has already been mentioned. It will be obvious that many factors will control the depth of soil and, conversely, many of the physical features of the soil will depend upon its depth. Most important here is the influence of depth on water content. Shallow soils always tend to be lacking in water, not only because evaporation to the air dries them out quickly but also because water is not easily

held. On the other hand, exceptional depth of soil may affect plant distribution by allowing the proper growth of the larger forms of life. Some of the very largest trees, for instance, seem to be restricted, as might be expected, to regions where the soil is particularly deep.

The most characteristic feature of soils and that which causes the most obvious differences between them is their texture, by which is meant the size of the particles of which they are composed. In local soils the process of weathering will tend to produce particles or masses of almost every size from stones downwards, and such soils are generally characterised by this heterogeneity.

In transported soils, as well as in some kinds of local soils, this is much less marked and they are characterised by homogeneity. This is obviously true of sand-dunes and alluvium for instance, where there is in the process of transport a gradual gravitational sifting. It does not, however, prevail so widely in glacial deposits, as the very name boulder clay testifies. The importance of the nature of the rock in local soils is clear in clays, which are themselves only hardened and ancient alluvial deposits and which thus tend when weathered to produce a homogeneous soil.

Some substrata consist entirely of masses of stone dimensions, as, for instance, the detritus sometimes seen on the tops of mountains and in such situations as pebble beaches. Conventionally, however, these are not regarded as soils and from the plant point of view at any rate may be regarded as discrete rock surfaces. In so far as they form a substratum for the growth of plants it is in virtue of small quantities of finer material which in course of time accumulate within them but which may be foreign to their constitution.

The three constituents which in fact control, by their proportionate representation, the physical nature of the soil are sand, clay and humus. Each of these plays a considerable part in determining the two main structural features of soil, its texture and tenacity. Their effect, however, is nearly always intimately connected with the water relations of the soil and can scarcely be divorced from them.

The presence of much sand, by which is meant here particles of medium size, leads to a loose and easily broken soil. The presence of much clay produces a dense, stiff, tenacious soil. Humus, which is itself essentially heterogeneous since it is composed of more or less decayed organic tissues, has in general a moderating effect and, while binding sandy soils, loosens and opens clays.

Apart from the fact that loose soils provide a less satisfactory anchorage for plants, texture affects plants chiefly in relation to water and air. Sandy soils with little or no humus allow water to percolate through at a maximum speed and with a minimum retention, and such soils are therefore more or less physically and physiologically dry. Clays, on the other hand, not only hold large quantities of water because of the surface effects of their small particles, but are often actually impervious to its passage. Thus unless there is considerable evaporation clay soils easily become water-logged. Similarly the coarser a soil the more adequate is likely to be its aeration.

The way in which water is actually held in soil offers a very difficult problem and can be considered here only in relation to the absorption of water by the plants. On this basis it is customary to recognise the water in soil as of three categories. First, there is the continuous liquid water or free water which actually forms the water table. Second, there is capillary water which adheres to the soil particles

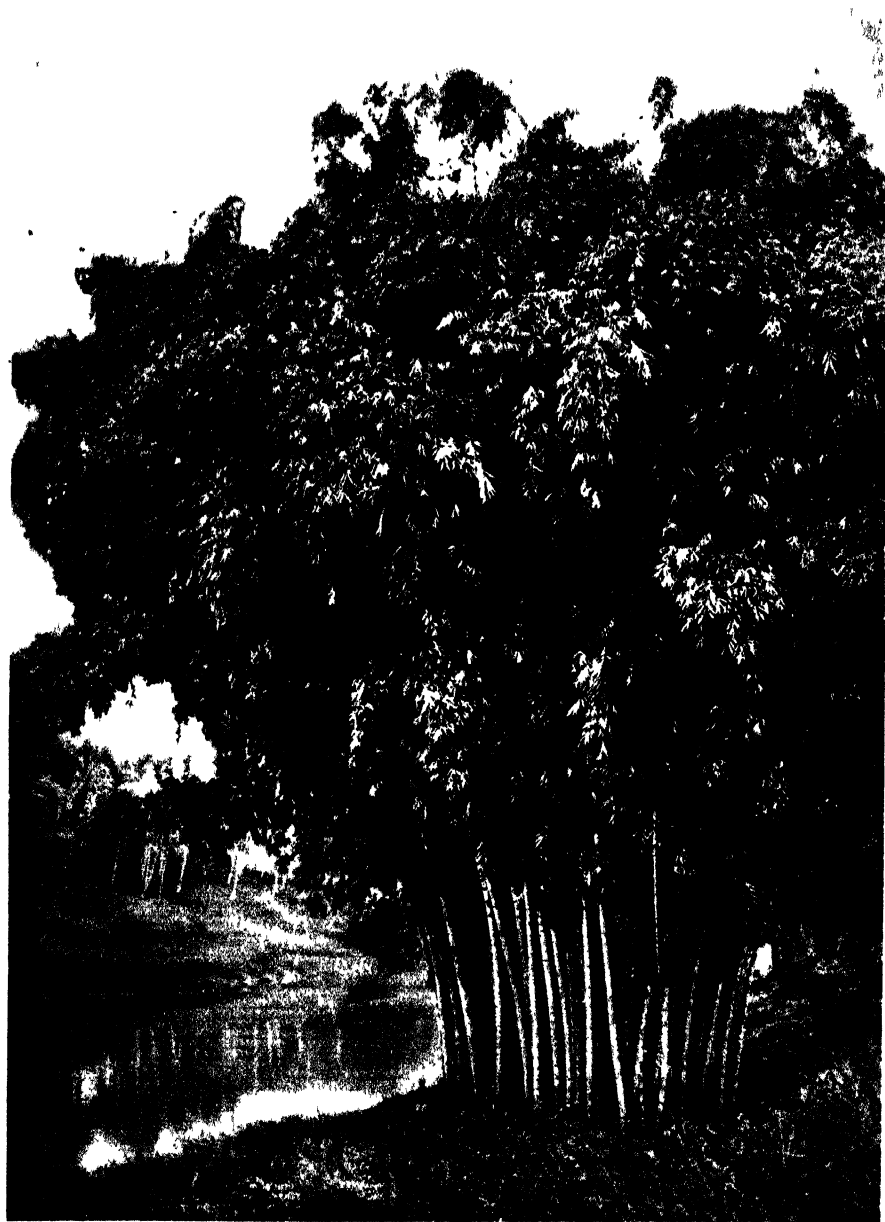


Plate 22. An Asiatic Giant Bamboo (Dendrocalamus giganteus)

(from Karsten & Schenck, Vegetationsbilder)

and which tends to move gradually by capillarity to wherever the soil is drier (normally towards the surface). Third, there is hygroscopic water which clings to the particles so closely that it does not travel by capillarity and which in fact can only be removed by such processes as boiling. To these three there may be added a certain amount of water which is chemically combined with certain compounds in the soil.

Soil in which there is a great deal of free water may be described as waterlogged. Soil in which there is little or no free water but a reasonable supply of capillary water may be called moist, and it is the gradual loss of this capillary water which marks the change from moist to the condition which we call dry. This ordinary conception of dryness however is but a relative one, and when a soil appears dry to the human senses it normally still contains an appreciable amount of capillary water. This is demonstrated by the fact that it is in general only the capillary water which is available for plant use and absorption, and it is a matter of common observation that plants can continue to live for varying periods in soil which appears to be "dry." It must not be supposed from this that plants make no use of other water, but on a simple view the water easily available to the plant may be considered to be the capillary water only. The free water will, of course, provide a great reservoir of this.

It is particularly in regard to water that humus plays a part. The very structure of small masses of vegetable matter is such that they act as minute sponges and retain, by capillarity, water which otherwise would easily be lost. So the presence of humus in the soil adds greatly to its water-retaining power, and in sandy soils this is often a very important point.

The impermeability of clay soils has been mentioned. One rather special effect of this is that in basins of such soils standing water may accumulate readily as ponds or lakes, and thus produce locally an entirely new kind of habitat open to occupation by species very different from those characteristic of clay soils.

Another most important physical feature of the soil is its temperature. This may be considered for all practical purposes as due entirely to solar radiation, except for the possible occurrence of exothermic chemical reactions in the soil. Soil temperature is becoming more and more recognised as a factor in distribution, and this is almost entirely in relation to the absorption of water by the plant. The process by which this is actually accomplished is too complex to be described here, but it can be said that it appears to be strictly conditioned by soil temperature. As a result of this, soils in which the temperature is low may, although holding copious supplies of water, be to the plant as if they were deficient in water. In other words, the water is there but is not available to the plant, which suffers as a result from what is called "physiological drought." This state of affairs must almost necessarily obtain where the water of soil is actually frozen, as it is more or less permanently in very high latitudes, but since the optimum temperature for water absorption in the plant may normally be regarded as appreciably above freezing point, this limiting factor has a much wider application in practice.

The chemical constitution of soils is a most intricate subject because of the immense range of chemical compounds or minerals that occur in nature. All the solid elements as well as many of the gaseous ones occur in the crust of the earth, and hence often in the soil, and many of these in a variety of combinations.

A review of the detailed facts of plant distribution shows that a great many minerals react favourably or unfavourably on the presence or absence of various plant species, and Hayek (114), among others, has given a long account of plants whose distribution is correlated with the occurrence of definite chemical compounds, particularly some of the metals, but in general there are in soils four chemical constituents of special importance in this direction.

These are quartz, of which sand is largely composed; aluminium silicate, which is the chief constituent of clay; calcium carbonate, which contributes largely to the formation of chalk and limestone; and humus, which comprises a wide range of organic compounds. These are the most widespread of all chemical soil constituents, and their proportional representation is the chief chemical distinction between soils, on which is based the broad classification of soils into sandy soils, clay soils, calcareous soils and organic soils. Each of them may occur almost to the exclusion of others, but more often soils show a combination of two or more and a preponderance of one or other. The correlation between this broad classification and the distribution of plants is very marked. The species of sandy soil are in general different from those of clay or limestone, as are these from one another. Similarly, where the humus constituent is preponderant still other species occur. Where, as in many soils, the constituents are well mixed, there is a similar admixture of species in the flora. Innumerable instances of these conditions might be given, but they formed a particularly important part of the chapter on the distribution of plants in Dorset (Chapter 13), and reference may be made to that account for particular examples.

It must not be supposed, however, that the physical and chemical features of soil are necessarily separate conditions. Indeed there are strong indications that they are intimately connected. In particular it seems clear that the importance of certain chemical features of the soil lies, from the point of view of the plant, in the physical conditions which they produce. It is familiar to find species that occur exclusively either on limestone or on sandy soils, but there are many which inhabit both. The common harebell, *Campanula rotundifolia*, is an instance of this. It is a normal constituent of the flora of many chalk or other limestone grasslands, but is also common on some soils of almost pure sand, and it is difficult to explain this except on the view that these two types of soil tend to provide the same physical conditions. This is true also of certain other species commonly associated with chalk pastures.

In turn the physical state of the soil influences its water relations and its temperature, and the general conclusion is that chemical and physical conditions must not be regarded as essentially distinct but rather as contributing equally to the general character of the substratum (8).

The question of humus is rather different, and is of great interest and significance. The waters of ordinary inorganic soils are in themselves either neutral or slightly alkaline in reaction. On the other hand, humus is to a greater or less extent acid in reaction. This is due partly to the secretion of acids from living plant roots and partly to the production of acids in the course of the decay of dead plant tissues. As a result the presence of considerable quantities of humus, especially in association with less alkaline mineral soils, tends to change the water reaction of the soil from alkaline to acid. This again is a very complicated chemical matter which can only be expressed here in very simple terms. The reaction of soil water in this way is due to its ionisation and to the resultant concentration of hydrogen ions.

Where this concentration is low the general reaction will be alkaline ; where it is high the reaction is acid. The hydrogen ion concentration is denoted by the letters *pH*, and the values are given mathematical expression in such a way that the greater the alkalinity the higher the *pH* figure, and *vice versa*. Neutrality is roughly indicated by the value 7, so that reactions of value above this are alkaline and below this are acid.

In practice the result will be an expression of the amount of humus and the natural reaction of the soil minerals, and in fact these considerations lead to a very wide range of *pH* values in different soils. Particularly, however, is this the case where humus is plentiful and the modifying effects of minerals are slight, as, for instance, in peat soils. Here the acidity may be very high.

As a practical issue in plant distribution it appears that the correlation of species with the *pH* of the soils in which they grow is very close, and that the segregation of species on this basis is very clear-cut. This point too is well illustrated by reference to the British flora.

The great majority of British plants grow in situations where the soil reaction is either about neutral or on the alkaline side. A comparatively small number live only where the reaction is definitely and sometimes markedly acid. So clear is this distinction that it is no exaggeration to say that it is by far the most conspicuous example of segregation according to habitat. It is true that the bulk of the species of the flora vary greatly in the degree to which they can stand acid conditions, and in places where the values fluctuate about neutrality or where there is but slight acidity many of these plants will occur, but no more than a handful of species can stand conditions where the acidity is high, and these never occur except in such conditions. In Britain high acidic values are to be found chiefly if not only in water-logged humus soils lacking in modifying minerals, namely in peat-bogs, and it is here that the acid-loving plants are found to the exclusion of all others. So obvious is this that it suffers from the familiarity that breeds contempt, and it is important to emphasise its interest. In any attempt to classify the facts of plant distribution in terms of the habitat such as was made in Chapter 13, the extreme segregation of these acid plants will be one of the most obvious features, and indeed it is not too much to say that only here is there to be found any invariable and unmodified correlation between habitat and range. It would seem indeed as if species, at least in Britain, can be divided into two groups most easily according to their relation to soil acidity, and no other basis seems to give so clear a segregation.

The explanation appears to be that these exceptionally acid habitats are essentially extreme and apart and are characterised by certain very particular and peculiar features. For this reason they are inhabited only by certain equally peculiar and specialised species which by reason of that specialisation find there, and there only, the conditions necessary for their growth. As illustrating the sort of conditions which this specialisation may entail, it is significant that all the so-called insectivorous species of our flora, the species of *Drosera*, *Pinguicula* and *Utricularia*, are restricted to markedly acid habitats. Just in so far as this specialisation may fit species for extreme conditions, so it normally may be expected to unfit them for more ordinary conditions, and this is certainly indicated by the extreme edaphic restriction of these acid-loving species.

To some extent the marked observed segregation in terms of soil reaction is due to the fact that the point of neutrality is by no means in the centre of the whole

gamut of conditions. That is to say there is a wider range of values on the acid side than on the alkaline. Associated with this it might be expected that more species would be able to exist throughout the whole alkaline range than throughout the whole acid range, and that there would be less likelihood of visible segregation in terms of alkalinity than in terms of acidity. This is supported by the fact that while it is very difficult to arrange species in terms of what may be called "alkalinity tolerance," it is comparatively easy to arrange many species in terms of their acidity tolerance. In rather different terms, it is easy to find species which are rough guides to acidity of the soil, but it is not easy to find species which are equally trustworthy guides to alkalinity.

Extreme values of alkalinity are, however, associated with a special soil condition which does markedly affect the distribution of plants. These are the soils in which sea-salt attains a considerable concentration. The plants able to live in such soils are called halophytes and they do not normally occur in other habitats. They are in fact specialised in much the same sense as the acid plants mentioned above, but perhaps in a lesser degree. They habitually show the morphological characters associated with an inadequate water supply, and are xerophytes because the concentration of the salt in the soil interferes with the absorption of water by the roots, so that these plants live in a state of physiological drought. Most halophytes can to some extent live in habitats of ordinary salt values, and to that extent their occurrence in maritime situations is facultative rather than obligatory. It is interesting to note that they occur also commonly in inland salt deserts or pans, and this suggests that it is indeed a matter of the soil salt that controls their distribution and not any other factor connected with the proximity of the sea. They are thus to be sharply contrasted with those species, mentioned in Chapter 13, which appear to owe their distribution partly to the distribution of salt in the atmosphere.

Biotic edaphic factors comprise all influences of other organisms on the habitat, though they chiefly concern in practice the activities of the bacteria of the soil, which control the rapidity or slowness with which humus may be formed as well as such chemical reactions as nitrogen fixation. The bacterial content of soils indeed is a very important measure of their general fertility, and the lack of this proper content is certainly the cause of the failure of many species to maintain themselves in the lighter, and what are generally called the poorer, soils.

Under biotic factors must also be included mycorrhiza, which is the name given to the symbiotic relation between certain flowering plants and fungi. In some plants the fungus permeates even the tissues of the seed and thus is kept in readiness for its germination, but in others the seed does not carry the fungus and successful germination depends upon the presence of the latter in the soil, whence it may come into association with the seedling at an early stage. In such cases as these the distribution of the species may easily be limited by the absence of the appropriate fungus in the soil. Some of the terrestrial orchids illustrate this condition.

In addition to these two main types of biotic factor many others will no doubt suggest themselves to the reader. Earthworms, as Darwin pointed out, play a great rôle in mixing and aerating the soil and altering its physical condition, and other animals do the same thing on a slighter scale. There is also the question of animal excreta. At least in the south of England certain plants tend

to be associated with rabbit-burrows and warrens in a way that strongly suggests that it is the result of the locally enhanced nitrogen values in the soil. Such plants include *Bryonia dioica*, *Myosotis arvensis*, *Urtica dioica*, *Cynoglossum officinale* and *Verbascum Thapsus*. Similarly the flora of manure heaps and of chicken runs is generally very characteristic.

CHAPTER 18

THE FACTORS OF DISTRIBUTION—IV. THE DISPERSAL OF PLANTS

AN enormous and very scattered literature has grown up round the subject of dispersal, and Ridley (203) has done botanists, and indeed all biologists, a great service by collecting together and publishing in one volume almost all the available information on the subject. This work is the source of much of what has to be said on the matter here.

The chief theoretical aspects of plant dispersal have already been dealt with, but it is desirable to review shortly at this point the various actual methods by which it is brought about, and the best way of doing this is to give first a tabulated list of them and then to make what further comments may be necessary about each.

Ridley classifies the main methods of dispersal as follows :

1. WIND—

A. Without special direct structural modification :

- a. tumble weeds ;
- b. dust seeds ;
- c. jactitation.

B. With special structural modification :

- a. winged disseminules ;
- b. plumed disseminules ;
- c. woolly disseminules.

2. WATER—

- A. Rain-wash.
- B. Ice, rivers, floods.
- C. Sea.

3. ANIMALS—

A. Internal carriage.

B. External adhesion :

- | | | |
|--|---|---|
| <ul style="list-style-type: none">a. simple adhesion ;b. special adhesive methods ;c. viscid adhesion. | } | <ul style="list-style-type: none">a. mammals ;b. birds ;c. other animals. |
|--|---|---|

4. MECHANICAL—

- A. Explosive fruits.
- B. Elongated stems, etc.

5. HUMAN AGENCY.

Tumble weeds.

Normally the seed falls from the parent plant when ripe either separately or in small groups contained in fruits, but occasionally the whole plant comes loose from the ground and is capable of being blown along the surface carrying its disseminules with it. Such plants are called tumble weeds. It is interesting to note that they occur especially or entirely in steppes and other open situations. *Psoralea argophylla* of the North American prairies and *Anastatica hierocuntica* of the North African deserts are good examples.

Dust seeds.

Given the occurrence of wind, it must follow that many plants will tend to be dispersed by this means, merely in virtue of the small weight of their seeds, especially if their shape also is such as to favour this.

Small light seeds occur in a number of families, but they are particularly characteristic of the orchids. Some idea of their size may be given by the statement that some species may produce as many as several hundred million on one plant, and that individual seeds may weigh as little as two-millionths of a gramme. Ridley gives an interesting account of the occurrence of orchids on remote islands, but it is noteworthy that there are quite a number of islands in which no species occur, and one obvious possible explanation of this is in the direction of the wind. This point is of some interest in relation to the general opinion expressed earlier that the possession of good dispersal means does not necessarily lead to effective dispersal in all directions.

Jactitation.

This is the term given by Ridley to the process by which seeds are scattered by being shaken out of the parent plant under the influence of wind. It is perhaps more popularly known under the phrase "censer mechanism." It may be said to occur to some extent in all plants which have dry dehiscent fruits and which are without any more definite methods of dispersal, and it is of special interest in view of the earlier discussion because it is a restricted method of dispersal whose chief effect is obviously to spread the seeds outside the shadow of the parent. It is seen in a number of very familiar plants, as, for instance, *Melandrium* (*Lychnis dioicum*), *Scilla non-scripta* and many species of *Papaver*.

Winged fruits.

Ridley points out that the presence of wings on fruits is not always associated with dispersal, and instances *Begonia*, where the fruit is winged but in which dispersal is related to the minute size of the seeds. Nevertheless in most winged fruits the wings serve as dispersal mechanisms, and the following types can be recognised.

In bladder fruits the carpel walls become thin and papery so that the whole pod can be blown about and, incidentally, will usually float. The bladder senna of gardens, *Colutea arborescens*, is a good example. In some plants the calyx develops into a thin bladdery covering to the fruit.

Winged or angled fruits are common. Conspicuously four-winged fruits occur in *Combretum* and in *Terminalia*, but the number of wings may be anything from two to a dozen. In the genus *Pentace* the number of wings is a useful specific character.

Fruits in which only a single wing is developed are usually called samaras, and this type is well represented among British plants. Everyone is familiar, for instance, with the "keys" of the sycamore and maple, and others are found in the ash and the elm. Sometimes, as in the first two, the fruit as a whole is really two-winged but splits into two disseminules each with one wing. Samaras are also common in tropical plants.

Nearly allied to the last in function are the bract wings which occur in a number of fruits such as those of the hop, the hornbeam and the lime. Another interesting instance is that of *Scabiosa*, where the wing is circular and resembles a pappus but is actually an outgrowth of the ovary.

A rather special condition of the last is seen in members of the grasses and sedges, where the special type of bract associated with the flower often acts as a fruit wing in dispersal.

Rarely the pedicel is flattened out into wings, this condition being particularly associated with the genus *Brunnichia*.

A fairly common condition is for the sepals of the flower to become enlarged and more or less membranous in fruit, and thus to provide wings of value in dispersal. This is particularly well seen in the family Dipterocarpaceae, where the wings and fruit are sometimes of great size, so much so that it would seem that the function of the wings can be no more than to control in some measure the fall of the fruit to the ground, and it is significant in this view that many of the members of this family are very tall forest trees. The same thing, however, occurs often in climbing or herbaceous plants and is no doubt associated with wider dispersal.

The much rarer condition of petaline wings occurs chiefly in tropical plants, but is found to some degree in many species of *Erica*. In *Calluna* there is a combination of winged sepals and winged petals.

Finally, it must be remembered that any organ, if sufficiently light and extensive, may assist in the dispersal of fruit or seeds.

Winged seeds.

These are in general not so common as winged fruits, perhaps, as Ridley has pointed out, because the only structure which can easily become winged is the seed coat. There are, however, many beautiful and well-developed instances, some of the finest being associated with the family Bignoniaceae. This is a tropical family, but *Catalpa*, which shows the condition excellently, is frequently grown in gardens. The genus *Dioscorea* also has well marked seed-wings. Among British plants the genus *Spergularia* is interesting as showing various stages in the development of seed-wings. It should also be mentioned that in many plants with minute seeds these latter are often winged (e.g. *Rhododendron* spp.), and it is a question whether lightness or the presence of wings is the more important in dispersal.

Plumed fruits.

In many grasses pluming, that is the presence of long silky hairs, is associated with the fruit or its related structures. *Phragmites communis*, which is often described as the most widespread Angiosperm, has such hairs well developed on the axis of the spikelet. On the other hand, Ridley comments on the fact that while such grasses are widespread on continental areas they are surprisingly rare on islands.

Plumed styles are not uncommonly developed and are conspicuous in a number of temperate plants, especially those of mountains. *Anemone* and *Dryas* exemplify the latter, and the genera *Geum* and *Clematis* are other conspicuous instances.

The subject of plumed sepals is almost entirely that of the pappus of the Compositae, which is so familiar and often-quoted an example of dispersal mechanisms. In these plants the calyx lobes are modified into bristles which may or may not be plumed, and the whole arrangement, as in the dandelion, is often very specialised. It should be pointed out that there are many Composites without this pappus development, and there is no evidence that their dispersal suffers in consequence. *Matricaria matricarioides* is an interesting example of this. A native of North America, it was introduced, presumably accidentally, into Britain in the latter half

of the last century. It possesses no pappus at all, but it has by now spread to practically every corner of the country. The Composites are, however, by no means the only plants with plumed calyx lobes, and the Proteaceae, especially the well-known silver tree, have them extremely well developed.

Plumed seeds.

Ridley points out that plumed seeds are always borne in capsules or follicles, and that they are specially characteristic of herbs or climbers rather than trees. Above all, they are to be found in the Asclepiadaceae and Apocynaceae, where they perhaps attain their greatest development in *Strophanthus*, but they are also well developed in the more temperate genus *Epilobium*.

Woolly seeds.

It is sometimes difficult to draw the line between plumed and woolly seeds as, for instance, in the seeds of the willows and poplars, but the condition is really characteristic and well developed in certain Malvales, where it provides some at least of the economic value of the cottons and the kapok.

Rain-wash.

Ridley, it is interesting to note, is of opinion that this is more important than is generally supposed because of the part which it may play in carrying the fallen seed further away from the mother-plant. It must in ordinary circumstances be of comparatively little general significance, and it is difficult to visualise any extensive carriage by this means. It seems likely to have particular application in the colonisation of newly formed land.

Ice, river and flood.

It is clear that moving water in whatever form will tend to have the same effect on disseminules as it may have on other objects, and hence that it must be a dispersal means to some extent. In the case of ice it has long been suggested that icebergs may transport disseminules, but this is an instance of a theoretical conception whose practical application can scarcely be regarded as other than very slight and, indeed, can hardly be more than accidental in occurrence.

Rivers will certainly assist plant dispersal in one direction and floods will tend to assist it less directionally. In these there is a general tendency to dispersal merely by the power of water movement irrespective of whether the disseminule can float or not, and there is also the particular aspect of dispersal of aquatic plants in the vegetative form of pieces of stems or buds, a method not generally applicable to land plants. The question of what may be called special water dispersal mechanisms involves the problem of flotation, and there is no doubt that many seeds and fruits are capable of floating in fresh water for a considerable time. Often this effect is produced by structures which are properly to be associated more particularly with other means of dispersal, as is the case with many of the winged and plumed disseminules, which by their nature will also tend to float, but there are several directions in which structure seems directed solely to flotation. Such, for instance, is the nature of the pericarp in fruits and of the testa in seeds. Broadly it may be said that where the texture of these is such as to hold much air the disseminule will float for a longer or shorter period. It may also fairly often happen that in falling into water some air may be inevitably imprisoned in the cavities of fruits and thereby cause flotation. Ridley gives many examples of these things

and also a survey of flotation in different families. The general conclusion is that freshwater dispersal by flotation is comparatively common, but must also, by the nature of the case, be of but comparatively local importance.

Carriage by sea.

The obvious possibilities of sea carriage have made this one of the most studied of all aspects of dispersal, and readers will find the work not only of Ridley but also of Guppy (107, 108) of great interest here.

At first sight sea dispersal looks a most promising way of explaining many otherwise inexplicable distributions and especially of many wide discontinuities, and so before going into any details it is important to emphasise certain general limitations inherent in the method.

In the first place, sea carriage differs fundamentally from freshwater carriage in that the actual medium of transport is more or less toxic to most disseminules. In other words, most seeds are killed by anything like prolonged immersion in sea water. Cases of great resistance to this danger are often mentioned, but these exceptions only prove the rule. Secondly, sea carriage must be correlated almost entirely with currents and hence will tend to be in certain directions only, and these are by no means the ideal theoretical directions. Again, most currents tend to have at least some north and south direction, and thus will tend to transport disseminules into different climatic zones. Thirdly, only a very small number of plant species are likely to disperse their disseminules into the sea, and, most important of all, sea carriage is very unlikely to deposit disseminules in spots where they can germinate and establish themselves. For instance, a plant growing on the slopes of a continental mountain is not likely to disperse its seeds into sea water. Still more unlikely is it that sea will disperse those seeds to the slopes of a mountain.

As Ridley's very long and detailed account shows, there are undoubtedly many species of plants which are by various peculiarities of structure and resistance capable of floating unharmed for long periods in sea water, and which therefore may suffer transport over vast distances by the action of sea currents. It is not surprising that the plants so widely spread on tropical beaches or throughout small tropical islands, such as the so-called strand plants and the palms, possess in greater or lesser degree such features. The coconut, for instance, is obviously designed to float unharmed in the sea. It is also not surprising that the strand plants are mostly very widespread, because they inhabit places to which the action of the sea can bring their disseminules. On the other hand, it is very significant that these strand plants are in general either tropical or (more rarely) temperate. There are few, if any, subcosmopolitan strand plants. Similarly it is very significant that the palms show an extraordinarily high degree of insular endemism, so that their power of flotation, instead of being associated with exceptional wideness of range, is in fact associated with the reverse. For instance, the fruit of the double coconut, *Lodoicea*, is frequently found floating in the sea and can undoubtedly do so for long periods without injury. But the plant which produces it is one of the palms found only in the Seychelles.

In short, in the opinion of the present writer the case of sea dispersal more than any other puts the general potentialities of dispersal in their right perspective. Where all the associated factors are favourable it may be of immense importance and allow a species to cover enormous distances, but this optimum condition is likely to be rare.

In the first place the disseminule must reach the sea, in the second it must be capable of floating, in the third it must resist the action of salt water, in the fourth it must be deposited, at the end of dispersal, in a suitable climate, and lastly in a suitable habitat for germination and establishment. It may be left to the reader to conclude how often all these conditions are likely to be fulfilled, and a reference back to the distribution of marine and semi-marine Angiosperms may be of assistance (Chapter 11). The distribution of the mangroves is particularly illuminating in this connection, in the way that they indicate that there are many considerations besides mere passage by sea transport which limit their ranges.

These observations must not be interpreted as belittling the interest of many aspects of sea dispersal. The structures which enable disseminules to float or which protect the embryo are often most intricate and beautiful, and Ridley gives a most interesting account of them.

So far attention has been drawn only to plants whose disseminules are capable of independent flotation. It has often been suggested that many seeds, especially if small, may be transported more or less accidentally in drifting wood or in pumice. The possibility of this in special cases must be borne in mind, but enough has been said to show that it is likely to be but very rarely efficacious.

It may also be remarked in relation to the mention of the coconut above that the exceptionally wide area of this plant to-day is certainly largely due to the influence of man.

Dispersal by animals.

As was indicated in the table on p. 294, animals tend to disperse disseminules in three ways, by swallowing them, passing them through and out of the digestive tract, by carrying them attached to their outer surface, or by carrying them in mud adhering to their feet, and, as Ridley points out, all animals thus may disperse plants to some extent. The primary consideration must naturally be the movement of the animals themselves, and this must always be borne in mind in gauging the importance of such dispersal. Locally restricted animals, or animals relatively immobile, will not play a large rôle. Generally speaking the problem involves mammals and birds, and the latter are of vastly greater potential importance because of their greater range of action. Grazing mammals, on the other hand, are probably responsible for a more intensive type of dispersal, because their food will always contain a certain number of disseminules and these will be almost continuously passed out of the body.

The structure of disseminules is correlated with animal dispersal in two main ways. On the one hand there is the development of the fruits so as to make them attractive to animals, which in consuming them will also consume the seeds, and on the other there is the development of special structures which will enable the disseminule to adhere to the surface of the animal.

Attractiveness to animals in turn is generally due to one or both of two features, namely colour and palatability. Colour may be in the fruits themselves, or in associated structures such as parts of the inflorescence axes, or in the seeds, as for example in arils.

Bird dispersal.

Dispersal by birds is generally associated with brightly coloured fleshy fruits such as form the main diet of many birds, but small dry seeds and fruits such as those of grasses are also eaten, and no doubt dispersed to some extent.

As with sea carriage, so also has bird dispersal received great attention because it promises to provide an explanation of much in plant distribution which is otherwise difficult to understand, but it seems doubtful whether it is capable of doing all that is sometimes claimed for it. There are many factors which will decide the value of bird dispersal, and these must be taken carefully into account. One, the active range of the birds concerned, has already been mentioned. Attention has rather naturally been focused on birds which are known to fly long distances, such as the migrants, but these are comparatively few and most birds have a comparatively limited range of flight. This is especially the case with those in which territoriality is strongly developed. Again, migrant birds usually have very definite routes and these routes are generally north and south, that is to say between widely different climatic zones. This is probably the most important point of all, because there must always be the possibility that long-distance bird flight may, at least on rare occasions, have taken place in almost all directions, but unless such flight can result in the deposition of the disseminules in conditions suited to their development it must necessarily be of no account. Again, in some parts of the world, as for instance in much of the tropics, there is little or no bird migration.

Another very important consideration, especially in relation to possible wide transoceanic carriage, is the speed of flight and the time that a disseminule takes to pass through the body. In general this time is probably very short, perhaps at most a few hours, and whether birds can and do retain their intestinal contents for a longer period when in flight is still doubtful.

It has been stated that migratory birds habitually travel on an empty stomach, but this has been contradicted, and it would at any rate be difficult to maintain that they never do so. It is also important to note that most isolated oceanic islands are not visited to any great extent by migrant birds. Related to this also is that many of the most wide ranging sea birds are not fruit eaters. In Tristan da Cunha, for instance, the only frugivorous land birds are endemic species.

In short, it seems that dispersal over wide areas by birds is very much on a par with wide dispersal by sea. There is a great potentiality in it provided that all the subsidiary factors are favourable, but the details of the process are such that it is difficult to imagine that such totally favourable conditions can be anything but very occasional. It may be argued that even very rare wide dispersal will be sufficient, but here there is the overriding consideration already emphasised that dispersal must be followed by germination and establishment, and this is something quite apart from the mere question of transport.

There is, however, one direction in which bird dispersal has probably had a paramount effect on plant distribution. This is the case of certain freshwater aquatic plants such as the duckweeds (*Lemna*). As was shown earlier, these plants are tiny free-floating aquatics, some with an extremely wide geographic range. They have no dispersal mechanisms in the ordinary sense of the word, but their form is such that they can easily be transported by simple adhesion. At the same time they are no better equipped for this than many seeds and fruits, and their wide distributions are to be attributed not to any specially valuable dispersal potentiality but to some other factor. It is not difficult to imagine what this may be. Free-floating aquatics live in a *milieu* quite different from that of land plants, the essential distinction being the elimination of many of the most stringent climatic influences. For instance, fresh water normally shows a much narrower range of

temperature values than neighbouring land surfaces, and, more obviously still, the amount of precipitation is likely to be of much less consequence. In view of this it seems reasonably certain that the wide range of *Lemna* (and what applies to it applies also to some other aquatics) is due to the greater similarity between its habitats the world over and the consequent greater chances of survival and establishment after dispersal. Birds carrying *Lemna* will tend to rise from one sheet of water and to come down on another which, however far away, will tend to be fairly similar to that from which the bird came. Here, it will be seen, the chance of deposition in an unsuitable spot which is so likely in the case of land plants is almost eliminated.

Carriage on the feet of birds.

The researches of Darwin (52) on this subject have always made it a somewhat classic example of dispersal, but all that we need say about it here is that it is in fact very parallel with the carriage of disseminules inside birds, and in particular is controlled by those same general considerations concerning bird carriage which have been noted there.

Other animals.

As regards dispersal by animals other than mammals and birds, attention chiefly centres round the activities of ants, whose relation to plants in general and to dispersal in particular is a subject of great interest. All that can be said here is that while in certain circumstances almost any animal may be instrumental directly or indirectly in dispersing seeds or small fruits, the result can scarcely be considered to contribute appreciably to the general distribution of plants.

Special adhesion mechanisms.

Perhaps the most noteworthy feature of these is that they parallel very completely the structural modification associated with wind dispersal, the difference being that, instead of wings and plumes, hooks are developed.

Rarely adhesion may be by branches of the inflorescence, as has been noted in certain grasses and Cyperaceae.

Adhesion by armed bracts is commoner and particularly associated with Composites, where *Xanthium* and *Arctium* provide two excellent examples. Here the hooks by which the disseminule clings are developed on the phyllaries.

The glumes of grasses are often so furnished with hairs and hooks that they cling readily, and several of our British grasses have these, although there are more striking examples in the tropics. In addition to mere attachment the structures in some grasses are such that the fruits actually bore into the skin of the animal and become absolutely fixed. Presumably in this case, if it is indeed a dispersal mechanism, the seeds cannot germinate until the death of the animals. The genus *Stipa* affords several examples of this, and the writer has seen joints of imported mutton so thickly penetrated by the fruits that they have been condemned as unfit for human consumption.

Adhesive perianth segments, such as are found in some of the Amaranthaceae, are not uncommon, and, in particular, adhesive calyces are familiar. They are found, for instance, in many Composites, where the bristles of the pappus are modified into hooks, the genus *Bidens* being notorious in this respect. *Myosotis* is also a good instance, as anyone who has walked through a wood where *M.*

arvensis is in fruit will know. The Labiatae furnish many examples too. Here the teeth of the calyx are variously recurved so as to form hooks.

Hooked styles are also frequent, as in *Geum*, *Anemone* and *Ranunculus*. A special form of this method is also seen in the stiff-haired awns of the stork's bill (*Erodium*).

It is, however, particularly in fruits that special adhesion methods are developed and they are very common, sometimes attaining great development and specialisation. Indeed, almost every type of dry fruit may be found furnished with hooks of one kind or another. Most of our familiar native examples of special adhesion belong here, and among them *Sanicula europaea*, *Circaea Lutetiana* and *Galium Aparine* may be cited, all three of them being exceptionally and irritatingly efficient. Extreme conditions are best seen in the so-called grapple plants belonging to the genera *Harpagophytum* and *Martynia*. In the former the fruit is several inches long and furnished with robust long-hooked processes. In the latter one end of the fruit is produced into a pair of very long curved hooks.

Viscid adhesion.

In much the same way as with plumes, wings and hooks, many parts of the flower or associated structures may become sticky by exudation from glands, but most of these variants are too rare to need mention here and our attention may be confined to viscid fruits and viscid seeds.

In some fleshy fruits the pulp is so sticky that the seeds adhere to anything they touch. This is particularly well known in the mistletoe, but it occurs also in a number of exotic plants.

Another form of adhesive fruit is where dry fruits of various kinds, chiefly achenes, are furnished with sticky glands. Several Composites, including *Adenostemma*, illustrate this well.

Quite a number of seeds become viscid when wet by the development of mucilage from their surface cells. This condition has been noted in several British plants, but the best example is certainly *Plantago major*, in which the secretion of mucilage is very copious. Many of the species of *Juncus* and *Luzula* show the same character.

Explosive fruits.

In all the cases so far discussed the fruit has been a relatively passive agent in dispersal, but there must now be mentioned some instances where it takes a more active part. In all of them dehiscence of the fruit, instead of being gradual, is so sudden that the contained seeds are shaken out more or less violently, sometimes to a considerable distance. The exact method by which this is accomplished varies a good deal, but is in all cases due to unequal strain set up in the ripening fruit, a strain which is ultimately relieved by the explosive rupture of the fruit wall.

One of the best known though not one of the most striking is the gorse. On hot summer days the popping of the ripe pods is very noticeable. The genera *Oxalis* and *Impatiens* also furnish many instances, the familiar name "touch-me-not" given to a species of the latter being a well-earned tribute to the sensitiveness of its ripe capsules.

Hura crepitans, a tree of the Euphorbiaceae, and the squirting cucumber (*Ecballium*) are other very remarkable examples.

Other mechanical dispersal.

In his chapter on mechanical dispersal Ridley refers to the fact that many plants possess rhizomes, soboles or runners which do in fact play a kind of subsidiary rôle in dispersal because they give the plants some kind of mobility, in that they enable new fruiting branches to arise at some distance from the parent axis.

From the theoretical point of view it must be emphasised that this is not really a method of dispersal at all, because no actual spatial discontinuity is involved, but a method by which the parent plant extends its own body over the surface of the ground. In no case, as far as the writer is aware, does such a vegetative spread replace dispersal by seeds or fruits, at least under natural conditions. Its function also seems to be quite distinct from that of dispersal. The latter, as has been shown earlier, is designed to scatter the species and to be a method at least by which increase of range can be accomplished, and it is intimately bound up in conception with the protected resting stage of the seed. Creeping stems on the other hand, while they may in fact increase the area occupied by a species, would appear to have, as their main function, the occupation of soil at the expense of other species, often together with the secondary function of perennation. Hence it seems justifiable to regard the process of spreading by vegetative means as related more closely to the problems of competition rather than to the problems of dispersal, and on these grounds it is not considered necessary to go further into the matter here. It may, however, be worth noting that in some cases exceptional powers of vegetative spread are associated with exceptional powers of dispersal, as is the case with *Chamaenerion (Epilobium) angustifolium*, and this may perhaps be evidence in favour of the view expressed above.

Dispersal by human agency.

This is perhaps the most convenient place at which to consider shortly the whole question of the introduction of plants into new countries by the agency of man. As has been said, we are chiefly concerned in this book with the natural distribution of plants, but their accidental or deliberate introduction by man is now so widespread and so much vitiates the picture of natural distribution that some account of it is necessary. It has, moreover, a very definite bearing on many theoretical aspects of our subject.

In general it may be said that there is scarcely a country in the world where human activities have not led to the introduction and establishment of species foreign to that country, and the intensity of this introduction is roughly proportional to the extent of man's influence on the country.

The subject is therefore largely the story of the emigration of man from European countries and his colonisation of distant parts of the world, but this is not the whole of the story and introduction of one kind or another has accompanied almost every human movement. For instance, many tropical plants, especially those of Asia and Polynesia, have been carried far and wide by the migratory movements of the native races of the region, and the wide range of many such plants and the uncertainty of their place of origin is generally due to this. This type of introduction extends over a long period of time and many of its early stages are now beyond elucidation.

The other aspect of the subject, that of introduction by the migrating and colonising activities of white peoples, has a much shorter history and is more or less coincident with the great colonial expansions of the last two or three hundred years.

This in turn has two aspects which illustrate in themselves the two main types of introduction, namely deliberate and accidental. The first of these is mainly associated with outward movements of the more advanced races from their centres in the northern temperate regions, and the second is generally the reverse. The former also tends to provide some of the more conspicuous examples of introduction, although the latter probably accounts for the larger bulk of species transference. That is to say, deliberate introduction usually concerns a fairly narrow range of species, while accidental introduction may be contributed to from a very great number of species.

Although introduction into the more distant parts of the world may be regarded as a fairly recent process, more localised transfer of plants has been going on ever since mankind first began to move freely about the world. The status of plants in Great Britain illustrates this point well. Species have been entering the country for hundreds, and perhaps thousands of years, and many of them have now become so integral a part of the vegetation that it is almost impossible to determine their real status. In relation to this particular point, however, it must be remembered that introduction has been over comparatively limited distances and from areas not too widely different. Where transference is over much wider areas, and more particularly across the equator, there is not the same difficulty in distinguishing between native and adventive species.

Except for the doubtful cases just mentioned, the adventive species in such a country as Great Britain, for instance, are generally to be recognised because they inhabit only unnatural habitats, that is to say habitats which exist only by virtue of man's actions. Arable fields, roadsides, waste places, buildings and walls are the special homes of adventive species, and it is generally only in particular cases and after a long time that introduced plants succeed in establishing themselves as constituents of the apparently aboriginal vegetation.

This is an important point which has been emphasised by many writers (3), and there seems little doubt that the struggle of introduction *versus* native (exotic *versus* indigene) is much less in favour of the former than is generally supposed. The point already mentioned, that introductions tend to be restricted to disturbed ground, is very generally true and is indeed probably the reason for the idea that introductions prevail, because it leads to their appearance just where they will be most conspicuous to the human observers.

This has been demonstrated very distinctly for New Zealand (44), and the conclusion is that exotics have scarcely entered at all into the primitive vegetation. It is pointed out that they are nearly always plants of the lowland belt, and also that their growth forms tend to be different from those of the indigenes and to militate against their successful competition. At the same time it must be remembered that the history of introduction, at least of northern plants, is for the most part very recent.

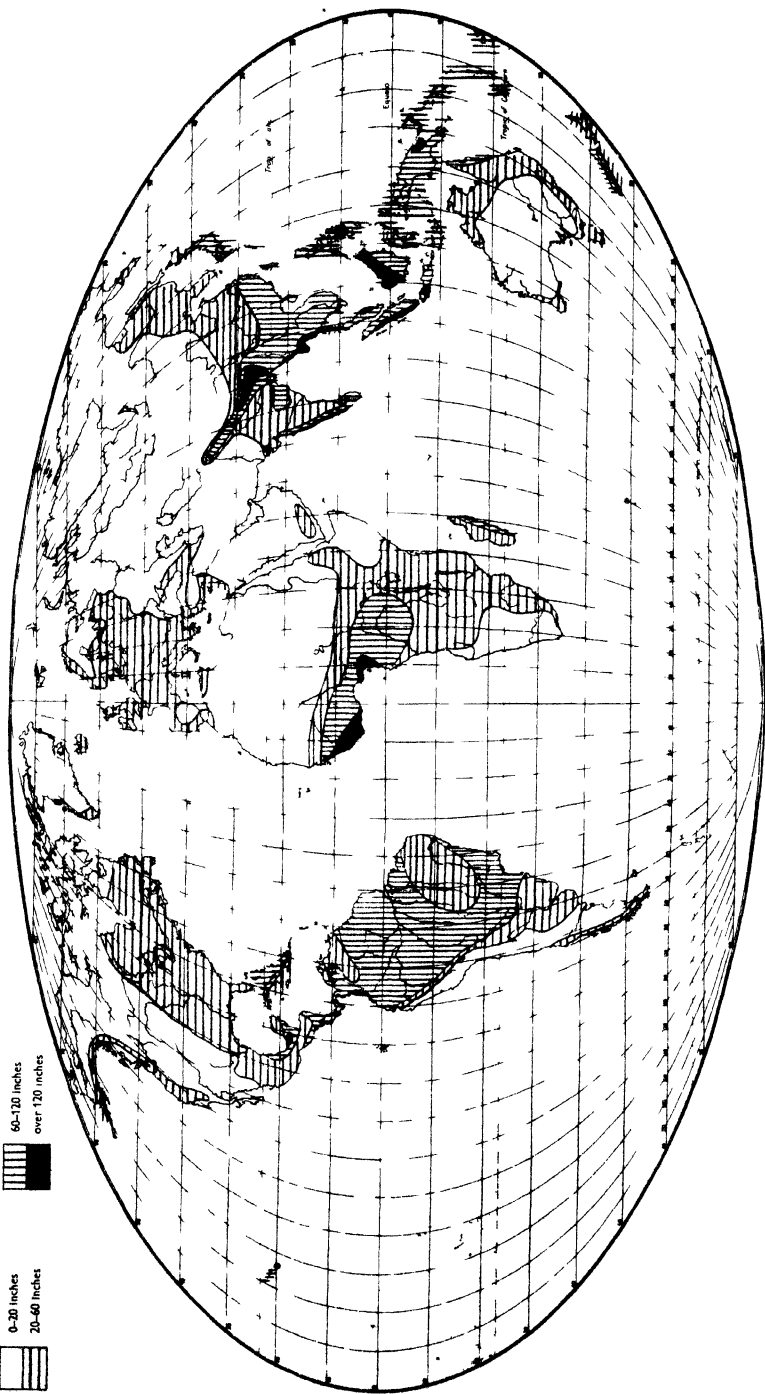
New Zealand has been the subject of a great deal of study in relation to introduction, and Thomson (245) has collected an enormous amount of interesting information, which will be reviewed in a moment.

The reason why introductions are mainly confined to disturbed ground is apparently that there the vegetation is open and the question of competition with existing plants does not arise, or only does so in lesser degree. In these circumstances of freedom from opposition the introduced species may flourish and multiply to an amazing extent, as for instance the *Opuntias* when introduced into Australia. Open water too provides the same freedom, and there

Map of the World showing the distribution of annual rainfall. Slightly simplified from various sources



PLATE 23



Areas correct Disortion increasing towards border of map
Approximate Scale 1 800 000 000 1600 miles inch along Equator
on Mollweides Homolographic Projection

are many examples of introduced freshwater plants luxuriating greatly. Two of the best-known examples are *Elodea canadensis* in England and *Nasturtium officinale* in New Zealand. Such plants, however, tend after a time to settle down to a more reasonable scale of existence.

Human dispersal of plants is of two kinds, deliberate and accidental. The former may obviously take all kinds of forms and there is nothing to be gained in analysing it further here, but in the latter certain circumstances are of special importance. These may be tabulated as follows :

1. Dispersal by accidental adhesion to moving objects :
 - a. Adhesion to man's person.
 - b. Adhesion to moving vehicles :

e.g. mud on cart-wheels, dust carts, trains, etc.
2. Dispersal among crop-seed :

e.g. many cornfield weeds.
3. Dispersal among other plants :

e.g. fodder and packing materials.
4. Dispersal among minerals :

e.g. soil export, ballast, road metal.
5. Dispersal by carriage of seed for purposes other than planting :

e.g. this includes a whole range of possibilities. One mentioned by Ridley is the spread of drug plants from the seeds escaping from druggists' shops.

So much for some of the more qualitative aspects of introductions. An idea of the quantitative side of the question is best conveyed by a reference to some particular country, and in view of Thomson's work just mentioned New Zealand may well be selected. The reader may also be reminded that the introduction of plants into Great Britain was dealt with at some length in Chapter 12.

The Naturalisation of Plants in New Zealand

According to Thomson (245) more than 600 species have been introduced into the country and have become more or less truly wild in the sense that they reproduce habitually by seed and have become permanent features of the vegetation.

A great many of these have become abundant or common throughout the country (274). They include many well-known weeds but also a few others, and the following is a list of some of them :

Ranunculus repens
Nasturtium officinale
Cardamine hirsuta
Capsella Bursa-pastoris
Silene quinquевulnera
Cerastium vulgatum
Stellaria media
Sagina procumbens
Spergula arvensis
Hypericum Androsaemum
Malva rotundifolia
Ulex europaeus
Sarothamnus scoparius
Trifolium pratense
Vicia sativa

Foeniculum vulgare
Arctium Lappa
Cirsium arvense
Cirsium vulgare
Chrysanthemum Leucanthemum
Bellis perennis
Senecio Jacobaea
Senecio vulgaris
Hypochoeris radicata
Crepis capillaris
Sonchus arvensis
Anagallis arvensis
Centaureum umbellatum
Digitalis purpurea
Mentha Pulegium

Prunella vulgaris
Verbena officinalis
Plantago lanceolata
Plantago major
Rumex Acetosella
Rumex crispus
Rumex obtusifolius
Chenopodium album
Euphorbia Peplus

Phalaris canariensis
Anthoxanthum odoratum
Phleum pratense
Polypogon monspeliensis
Holcus lanatus
Dactylis glomerata
Cynosurus cristatus
Poa annua
Poa pratensis

Of these *Hypochoeris radicata* is often considered the most ubiquitous of all. *Nasturtium officinale* and *Verbena officinalis* have occurred or still often occur in very large forms. *Trifolium pratense* (red clover) is of exceptional interest because its abundance is directly associated with the presence of humble-bees, which seem to be the only insects capable of pollinating it. These bees were deliberately introduced into New Zealand, and before their advent the red clover rarely if ever set seed. All the species mentioned are common European plants, and the only other species which has become widely established appears to be *Eschscholzia californica*, which, as its name implies, is a native of western North America.

Some species have become so completely established and form so intimate a part of the natural vegetation that they have often been considered to be native. They are, however, almost certainly introductions and include *Geranium molle*, *Sonchus oleraceus*, *Plantago Coronopus* and *Polygonum aviculare*.

On the other hand a number of species are much less common than might be expected. Among them are :

Papaver Rhoeas
Geranium Robertianum
Daucus Carota
Centaurea Cyanus
Cichorium Intybus
Calluna vulgaris
Convolvulus arvensis

Lamium album
Lamium purpureum
Urtica dioica
Urtica urens
Arrhenatherum elatius
Agropyron repens
Brachypodium sylvaticum

Others have become firmly established locally as garden escapes, as *Pelargonium zonale* and *Tropaeolum majus*. The peach, *Prunus Persica*, is of interest here too. In the earlier days it established itself freely, but now it does so far less frequently and seems to be restricted by the occurrence of certain diseases from which it suffers.

Perhaps more interesting than any of these are the plants which have never been able to establish themselves, even with the repeated help of man. *Viola odorata* and various species of *Primula* such as the primrose, cowslip and polyanthus are noteworthy examples of this, and the reason seems in some measure at least to be the absence of the normal pollinating insects. In the case of the *Primulas* the plants refused even to seed before the introduction of bees. They now do so in gardens but have never become established. Heaths of various kinds also have never been naturalised. Other species which, fortunately or unfortunately, have never become established are *Linum usitatissimum*, *Pisum sativum*, *Lathyrus odoratus*, *Petunia parviflora*, *Opuntia vulgaris* and *Scilla non-scripta*.

A group of species have become widespread only since the introduction and subsequent multiplication of such fruit-eating birds as thrushes and blackbirds.

The prevalence of the blackberry, *Rubus fruticosus*, which is perhaps the worst of all weeds in New Zealand, is a case in point, and others are *Berberis vulgaris*, *Rosa rubiginosa* (which incidentally is far more widespread than *R. canina*), *Crataegus*, *Ribes Uva-crispa*, *Sambucus nigra* and *S. racemosa*, *Leycesteria formosa* and *Phytolacca*. There are, of course, native fruit-eating birds, but presumably their natural diet is in general confined to native species.

In the course of his remarks Thomson refers frequently to the dispersal mechanisms of the various plants, and it is interesting to note that in the following species the seeds or fruits become sticky when wet: *Capsella*, *Lepidum sativum*, *Viola tricolor*, *Artemisia Absinthium*, *Senecio vulgaris*, *Gilia* spp., *Glechoma hederacea*, and species of *Plantago*.

Finally there are a few cases of special interest. *Brassica oleracea* was planted by the earliest visitors to the country, and the progeny of this stock has gradually reverted to the wild type, which now inhabits sea cliffs in various parts of the dominion as it does in Europe. *Matricaria matricarioides*, which has been referred to elsewhere, was locally abundant as early as 1882 and has since spread almost everywhere. *Verbascum Thapsus* is especially common where there are big populations of rabbits, a feature which is noticeable in its distribution in England also. The broad bean, *Faba vulgaris*, has been noted sprouting from the skeleton of a pigeon, the inference being that germination was possible only after the body of the carrier had decayed. Some people think that many seeds are distributed in this particular way.

Certainly the most conspicuous feature of the long list given above is the fact that practically all the plants mentioned are what may be called common European weeds belonging to what has been distinguished as the Scandinavian floristic element. The great prevalence of these as adventives not only in New Zealand but in almost all countries has been commented on again and again from the time of Hooker, who in his *Introductory Essay to the Flora of New Zealand* (126) discussed the matter at length. So impressed was he by this "aggressiveness and colonizing power of the Scandinavian flora" that he foresaw the gradual extermination of indigenous floras by these adventive species. This extreme point of view was no doubt connected with the fact that at first sight these adventive species appear much more ubiquitous than they really are, because they follow so closely in the footsteps of man, and it is fairly certain now, as Thomson and others have shown, that there is no likelihood of this eventuality. It would seem that it is not so much the inherent aggressiveness of the species in question as the advantages which their association with man confers on them. Man's actions tend to provide a series of habitats, those of disturbed ground, which are specially the domain of these plants and which do not occur in nature. This certainly leads to local destruction of the native vegetation and some native species inevitably become rare in the process, but Thomson has stated definitely, in respect at least of New Zealand, that he knows of no case where a native species has been completely exterminated by adventives, and his general opinion, as it is also that of others, is that when man's influence is removed the native flora can everywhere hold its own.

But there is also another very interesting aspect of this problem. The northern hemisphere generally and Europe in particular has been the stage of man's development for vastly longer than any southern countries, and the kinds of artificial habitats which this development produces have in the north been available for local plants for infinitely longer. May it not be then that the common northern

weed species are in fact species or strains peculiarly fitted for these habitats, and in fact slightly different from the corresponding forms which grow in natural situations? If this is so, then it might be expected that these weeds would flourish in all artificial habitats no matter where they might be, and would tend to produce the effect of aggressiveness observed. In this connection it is not without significance that a few plants such as *Festuca ovina* and *F. rubra* and *Cardamine hirsuta* occur in New Zealand not only as adventives but also as natives, and that in these cases the exotic is generally more prominent than the indigene.

THE FACTORS OF DISTRIBUTION—V. CHANGES OF CLIMATE

THE belief that climatic values have in the past fluctuated greatly with the passage of time is now so generally held as to have become almost axiomatic, but it is nevertheless desirable here to consider shortly the reasons that have given rise to it. For more complete presentations of the subject the reader may refer to the work of Simpson (219, 290), Brooks (29, 30) and Huntington and Visser (134).

The direct and indirect evidences for climatic variation in the past are of five kinds, namely, mathematical and geodetic, geological, botanical, archaeological, and meteorological.

The first need not detain us long because it is rather remote in all senses of the word from our present subject. It comprises the relations between the earth and other heavenly bodies, and also the question of the mode of formation of the earth and its subsequent vicissitudes, these being such that it is impossible to suppose that the present conditions of climate can have existed unchanged for any considerable part of secular time or of the earth's history. Indeed, there is reason to believe that for long after the formation of the world no climate in the modern sense existed.

Geological evidence of climatic change is of two kinds, the first being that afforded by the appearance and texture of certain rocks. Thus some sandstones appear to be formed of dune sand, while some Tertiary granites show signs of having been weathered by sand blasts, both suggesting that contemporary conditions were very arid (215). On the other hand many clay deposits can scarcely have been formed except under pluvial conditions. Not only are these rocks found where now the climate is very different from that indicated by their formation, but the various types may be found superposed or intermingled, showing that the climate of their region of deposition must have undergone considerable changes. Indeed a vertical section through almost any series of geological beds will show a variation of type that can only be explained by an equal variation of climate. Moreover, freshwater deposits will be found among and between marine deposits, indicating at least geographical changes such as are unlikely to have been without effect on climate.

The geological evidence of climatic change is, however, above all seen in relation to glaciation. Ice-sheets and glaciers scour and mark the surface of the earth where they occur in ways which leave unmistakable evidence of their former presence long after they have disappeared. The nature of these traces has already been described and it need only be remembered here that they are found over wide areas of the world where now the climate is far from polar.

Glacial conditions are now generally supposed to have been more or less widespread on the earth on a number of occasions during geological history, that is to say it is believed that there have been in the past a series of glacial epochs or ice ages. These were, however, separated by vast periods of time. Only two have occurred since the beginning of the Palaeozoic, and of these only the latter involves the Angiosperms and is therefore of more than passing interest to us here. As

will be seen, these glacial ages are to be regarded as long intermittent catastrophes in the general story of climate, and as such are perhaps the most striking evidence of the fact that climate has not always been as it is to-day.

The nature of the changes which accompanied the Pleistocene glaciation and their immense effect on the existing vegetation have already been described, but it may be reiterated that the climatic change at this period was of enormous extent and vast significance and has certainly been the main influence in the moulding of the world flora into the state that we now see, and this will be even more apparent at the close of this chapter.

There is another more indirect geological evidence of climatic change which may be mentioned here. Mountain ranges are one of the most potent influences in determining local climate in many parts of the world, because they intercept moisture-laden winds from the seas, thereby causing on their leeward sides not only conditions of drought but also many consequent climatic changes. It is fairly clear that mountain building on the grand scale has been particularly the characteristic of certain periods, as, for instance, of the Miocene, when most of the present high ranges were elevated, and that in the intervening periods relief was much less marked. This cannot fail to have had an enormous effect on the distribution of climatic values, and hence the very presence of mountain ranges of different ages is evidence of appreciable climatic change in the past. This point may be illustrated by the often quoted case of North America (19). Here there is abundant evidence that the elevation of the western mountain line radically altered the climatic values of almost the whole subcontinent.

The botanical evidence is similarly twofold, but by far the more important aspect is that afforded by the nature and characteristics of fossil plants. The question of the extent to which fossil floras are tests of climate has already been discussed in Chapter 14, and it is clearly dangerous to push conclusions too far, but it cannot be denied that in a broad sense the general appearance and structure of plants do to a large extent indicate the types of climate under which they flourish. To take the most obvious example, it is contrary to all experience to associate highly succulent plants such as the cacti with any but very dry climatic conditions. Unfortunately the problem of fossils is not so clear-cut as this, but they may nevertheless be very significant indicators of climatic values, and at least it seems certain, on their evidence, that temperate or warm-temperate conditions were formerly much more widespread latitudinally than they are to-day.

In particular they indicate that conditions of this kind must once have prevailed much further towards the poles than they do now, and indeed that they may have extended far into the arctic and antarctic. On matters of detail there is still a good deal of difference of opinion, but that this is true of both the northern and southern hemispheres is beyond doubt.

Fossil floras from the tropics in so far as they have been studied also add to the picture. They appear to be very like the floras in the same places to-day, and thus indicate that changes of climate in the past probably largely concerned the temperature gradients between equator and poles rather than absolute differences in world values.

The second and minor type of botanical evidence is that afforded by the annual rings of certain large and long-lived trees, especially the Sequoias of California. The width of the annual rings in trees is a rough measure of the amount of growth which the tree has achieved season by season. This in turn is generally supposed

to be a function of the climatic conditions, and especially of the precipitation. Developing this argument, it may be suggested that variation in width of ring will reflect and correspond to variation in rainfall from year to year. Examination shows that the rings of a large tree do in fact vary greatly in width, and also that this variation is a fluctuating one, the rings over one series of years being small and over another series being large. They tend in fact to wax and wane through the years, and this is generally interpreted as indicating a corresponding oscillation in climatic values. Naturally the length of life of any single tree is negligible in terms of geological time, but some of the big trees mentioned live for some thousands of years and thus cover comparatively long periods.

This subject of the correlation of ring growth and climate has received much attention, especially in the work of Douglass (60), and the general conclusion that there is something approaching a persistent fluctuation in climatic values is inescapable. Actually investigation on these lines has been pursued very intensively, and there have been built up on the basis of ring-size climatic curves for the area in which these trees live extending back for hundreds of years. These curves, as has been said, seem to show beyond doubt that rainfall at least has varied almost continuously during the period concerned.

It will be noticed that these various lines of evidence have gradually brought the problem of climatic change more and more towards the present time, and the next type of evidence, the archaeological, is almost entirely concerned with changes in recent, and especially in historical, time. In many ways this evidence is the most interesting of all, because the earlier ones concerned periods and events so remote that they necessarily seem a little unreal. With the archaeological evidence the question of climatic change becomes more tangible and realistic. On the other hand, the changes themselves are naturally smaller but not for this reason of any less interest.

At this point it is desirable to draw a careful distinction between climatic changes and climatic fluctuations, as there is some ambiguity in the use of these terms. The geological and botanical evidence has shown that there has been considerable long-term alteration in the climate of the world, and that this has included a series of catastrophic alterations. It is to these secular alterations and oscillations that the word change can be best restricted. Other botanical evidence has shown, and the archaeological evidence will also show, that in addition to these there have been constant minor variations, variations superposed, as it were, on the general trends of change. Major change seems never to have been quite smooth and unbroken but to have progressed in the form of irregularities. It is to these minor irregularities and variations that the word fluctuation is best applied. For instance, the general trend of climatic *change* since the end of the Pleistocene has been a gradual amelioration of condition, and this process has been sufficiently noted in Chapters 12 and 14. At the same time there have been almost constant *fluctuations* and advances and retreats in the main process of amelioration, and it is with these that we are now concerned. It must be emphasised that, although these fluctuations are minor compared with the main changes, they are nevertheless more than adequate to influence plant distribution, and indeed this may be the more normal way in which this influence makes itself felt. It must also be remembered that there is a close relation between change and fluctuation, and that the accumulation of the latter may and no doubt does often produce the former.

The archaeological evidences of climatic variation are very numerous but for

the most part inferential rather than direct. That many of them represent indeed some measure of change can scarcely be doubted, but the nature and extent of that change are often matters of considerable argument. We are not, however, concerned here with details, but rather in demonstrating that change of one kind or another has occurred, and for this purpose deductions on archaeological grounds are valuable and important.

These indications of climatic fluctuations are really of four types. The first concerns the relatively minor oscillations that have taken place in the north polar ice-cap during the historical period. In the Norse period settlements were established on both the western and eastern coasts of south Greenland, and there is evidence that a fairly well-developed agriculture was carried on there. Now the region is permanently glaciated and even habitation by Europeans is out of the question. Of special interest are the excavations which have been made in a burial ground attached to the settlement near Cape Farewell. The details and methods of burial here clearly point to a gradual oncoming of severe conditions leading eventually to the disappearance of the whole settlement. Similar minor recessions and advances of the ice are known from the Alps and other parts of Europe.

A second general indication of climatic fluctuations, and especially of rainfall, is seen in various directions where changes in the level of bodies of water can be estimated. The best known of these is the record of the annual level of the Nile, which is known from about A.D. 600 and which shows almost continuous fluctuation superposed on a gradual and steady rise.

Similar variations have been observed in the Caspian and in parts of North America, especially in the old lakes associated with the Pleistocene glaciation. In Africa there is the well-known shrinking of Lake Chad.

Another more general inference is that afforded by the distribution of some of the great city civilisations of the past. Mesopotamia contains the vestiges of civilisations which could scarcely exist there to-day in view of the dryness of the climate, and something of the same is suggested by the remains of the Roman cities in North Africa, which are in regions to-day so dry that it is difficult to imagine how a considerable population could be maintained.

A rather closely related example is that of the Kharga Oasis on the eastern edge of the Sahara. In earlier historical times the oasis was a lake which later degenerated into a swamp. Since then the water in the oasis has varied greatly, and its human occupation has waxed and waned also.

The reverse condition, of ancient cities now lying buried in dense tropical forests, and which seem to have been overwhelmed by an increase in precipitation, is seen well in the country of the Mayas in Central America. Here the cities appear to have been at their zenith about the first few centuries of the present era. Now, as Brooks says (30), "this country is at present covered by almost impenetrable forests, the climate is hot, moist, and enervating, while the inhabitants are idle and uncultured." A less familiar example is furnished by Angkor, the great abandoned city now buried in the tropical jungle of Cambodia. It was founded about A.D. 600 and flourished for the next 500 years or so, and at one time is estimated to have had a million inhabitants. It is thought to have been abandoned in about A.D. 1200.

This brings us to the last and most detailed evidence, that afforded by actual meteorological observations during the last 200 years or so. All such observations go to show that in most respects, and perhaps particularly as regards rainfall,

climatic values tend to fluctuate more or less continuously, a series of years below the norm being followed by a series of years above the norm. This at any rate is a general conclusion, and it can be substantiated in detail, particularly from very many meteorological records.

One aspect of this fluctuation and its effect on plant distribution has been studied in some detail (99). The lizard orchid, *Himantoglossum hircinum*, has an interesting geographical history in Britain, of which the main features are its fairly regular occurrence locally up to about the middle of the nineteenth century, its decline and virtual disappearance between that date and 1900, and its marked increase in numbers and range during the present century (or at least to 1933, when the study was made). So conspicuous is the last feature that enquiries were made to discover whether there was any appreciable minor climatic change in Britain about 1900, and the result of those enquiries (26, 31, 147) was to show that there was such a minor change, chiefly in the direction of seasonal temperatures, and, taking all the facts into consideration, it seems evident that the rapid recent extension of the plant has been made possible by this change.

On a still shorter scale the fluctuations of climate from year to year is in everyone's experience, and it is necessary to mention only the markedly hot and dry summers of the years 1933–1935 and the cold winters of recent years as instances of this.

The combined effect of all the lines of evidence which have just been reviewed has been sufficient to demonstrate beyond doubt the two main facts that climate has suffered changes both great and small, and that these have been reflected directly in the distribution of plants. We may now go on to see whether it is possible to give a more general picture of climatic change during geological time, and especially during the history of the Angiosperms.

This has actually been done with a wealth of evidence and detail by Brooks (30), and we cannot do better than describe shortly the conclusions to which he comes. Put very concisely, these are that the climate of the earth has normally been a genial climate interrupted only at long intervals and for short periods by glacial periods, "as at long intervals a passing cyclone disturbs the peaceful life of a tropical island." The long genial or warm periods were all periods during which the relief of the world's surface was low and during which, as a result, shallow seas encroached more or less extensively over the land surfaces. These periods too were characterised especially by comparatively small and gradual differences between the equator and the poles. On the other hand, the glacial periods seem to have followed periods of active mountain building and were characterised by steep and extensive temperature gradients from equator to poles.

One of these long warm periods apparently persisted from the glaciations of the Permian to those of the Pleistocene, and it was during this long time that the Flowering Plants were evolved. As regards these plants then, they originated during a long warm period, and these conditions continued to prevail for millions of years after they had appeared. Only comparatively recently from a geological point of view did these optimum conditions give place almost suddenly to one of the catastrophic periodic glaciations whose vibrations still persist.

This conception throws much light on the geographical development of the Flowering Plants. Arguing from it we are justified in regarding this great group of plants as developing in response to and in correlation with more or less constant and optimum climatic conditions, and perhaps as having reached towards the end

of this period what may be described as something approaching an equilibrium. With the onset of glaciation this equilibrium was suddenly and rudely disturbed. An almost completely new range of climatic conditions arose in the higher latitudes at any rate, conditions to which the Flowering Plants were quite unaccustomed, and their subsequent history has undoubtedly been the story of their attempts to accommodate themselves to their environment. It is to this more than any other factors that many of the more puzzling details in the present distribution of plants are due.

This point of view can be conveniently illustrated by a consideration of certain aspects of arctic plants. From the various evidences available it is an almost inevitable conclusion that during the long warm period of the Cretaceous and earlier Tertiary temperate or warm-temperate conditions must have been the rule throughout the upper latitudes, and that arctic conditions, that is to say glacial conditions at sea level, were unknown anywhere in the world. Apart from the circumstantial evidence afforded by fossil plants Brooks has shown that there is definite meteorological and mathematical evidence for this view. He shows, for instance, that even to-day a comparatively small rise in mean annual temperature of the order of 5° F. would be sufficient to cause the gradual melting of the polar ice-caps and to prevent them re-forming, and the temperature of the warm periods was certainly above this figure. Moreover, once the ice-caps disappeared their effects on the climate would be removed and almost certainly an even warmer climate would be the rule.

The essential feature of the glacial period of the Pleistocene as regards the Angiosperms then was to produce for the first time in their history what we now call arctic conditions, and these over a comparatively wide area. This being so—and there seems little reasonable doubt about it—several consequences follow. The chief of these is that cold-temperate and arctic plants must be regarded as comparatively recent in origin, and this element of the world flora as its youngest. The association of mountain building with glaciation also suggests that desert conditions have recently become much more widespread than they were in the warm period, and thus many of the more xerophytic plant types are perhaps to be regarded as young and recent. On the contrary, the general climate of the warm periods seems to have been characterised by fairly high temperatures and by moisture, and it may be expected therefore that types now associated with such conditions will be among the older and earlier developed. Such indeed is the direct evidence of fossil floras, although there are reasons why this point must not be pushed too far.

Reverting to the question of arctic plants, it must not be assumed that prior to the Pleistocene glacial conditions were entirely absent from the earth or that there were no plants growing in such conditions of climate. Glacial conditions pertain not only at sea level in the polar regions but also above the snow-line on mountains, and the distribution of mountains is such that on some at least the summits must have been glacial even during the warm periods—especially so since in the early Pleistocene the mountains thrown up in the Miocene were presumably higher than they are to-day. Even to-day there are snow-caps on some of the equatorial mountains, as on those of East Africa and on those of the tropical Andes. But the highest mountains are well scattered in latitude, and in latitudes as high as 60° N. there are in Alaska heights exceeding 20,000 ft. Whatever may have been the case on the equatorial mountains during the warm periods, it is impossible to believe that the general level of temperature was so high that there were not glacial

conditions on mountains over 20,000 ft. high in the neighbourhood of what is now the arctic circle. Actually they were probably fairly prevalent on the higher mountains of the world.

It would seem then that our survey of climatic change leads to another important recognition, namely that, while arctic conditions are probably very recent in origin, arctic-alpine conditions have probably existed for a very long time, and that consequently the relationship between arctic and alpine floras expresses the origin of the former from the latter rather than the reverse. This, it may be remarked, is fully in agreement with the distribution of their respective constituents.

Finally let us turn to the vegetation of the low-lying tropics. There are no indications either from fossil or other evidence that the maximum or equatorial world temperature has ever been appreciably greater than it is to-day. Indeed, on astronomical grounds there are *a priori* grounds for this view. The difference between the climate of the warm period and that of the Pleistocene was therefore, as has already been said, essentially the difference between a generalised latitudinal climatic zonation and a very steep zonation. In other words, the tropics in the warm periods were probably not warmer, but the higher latitudes in the glacial periods were much colder. In floristic terms it may be said then that while in the warm periods circumstances favoured the development of a few widespread and generalised plant types of which the present tropical flora is probably a good example, circumstances in the glacial periods produced not only a tendency towards the production of more specialised types in correlation with the more specialised conditions, but also brought about a world-wide telescoping of the climatic zones, so that if nothing else there must have been an intense struggle for space. This in turn no doubt led to further and more local specialisation, and thus the whole effect of the glaciation appears to have been to hasten the conversion of a generalised world flora into a number of more or less specialised floras. Certainly this specialisation is one of the main features in the world flora to-day, and it would seem that this at least is a partial explanation of it.

Attention has often been called to the fact that in continental floras where there is a high degree of endemism, as for instance at the Cape and in south-west Australia, the endemics are markedly associated with the more arid types of habitats, namely with that type of habitat which a survey of climate in the past suggests is of more recent origin. The proportion of herbaceous types among these endemics is also noteworthy and, according to some beliefs, indicative of their comparative youth. On the other hand, on oceanic islands, where the degree of endemism is high, the endemics are more frequently mesophytic woody types and may well be relics of the older moist forest floras of the world. Wallace (251), for instance, expresses his view that every island represents the fauna and flora of the period when it was last separated from the adjacent continent, while Guppy (109) has put the matter even more plainly where he says, "islands appeal to me more as registers of past floral conditions in the continents than as representing their present state. Their marked peculiarities bear the impress of the past on the continents, whilst their common features tell the story of the present."

Thus it seems reasonable to regard the changes in climate during the history of the Angiosperms as having led gradually to a more and more specialised series of local climates, particularly during and since the Pliocene, with consequent differentiation in the vegetation. This point has been well put by Bews (25), who says, "the evidence from phylogeny . . . affords convincing support to the view

that climatic differentiation has been responsible for the production of plant forms adapted to more open grassland conditions, to scrub, semi-desert and also, though this began very early, to the temperate flora as well."

This view involves the belief that the earlier Angiosperm flora was of a generalised forest type and very widespread, and that the development of vegetation as we see it to-day has been in the various directions of specialisation from this original condition. This is differentiation, and this particular aspect of Angiosperm history is, as we have seen, an important basis of Guppy's Theory of Differentiation.

CHAPTER 20

THE FACTORS OF DISTRIBUTION—VI. GEOGRAPHICAL CHANGES

THERE are few clearer illustrations of the bearing of the evolutionary conception on problems of plant distribution than that of the question of the importance of the distribution of land and sea. On the assumption that species were created in or near the situations in which they occur to-day, discontinuity of range is not necessarily of any great significance, because it can be explained on the assumption that creation took place on more than one occasion and in more than one place. If, however, an evolutionary origin of species is assumed with its generally accepted premise that species are monophyletic, then clearly the discontinuity of species becomes a matter of special interest and importance. It is not altogether surprising therefore to find that the pioneers of the idea of evolution realised almost from the first that discontinuity was a subject likely to hold the key to many riddles and paid special attention to it. More remarkable is the fact that even in those early days, and actually antedating the *Origin of Species*, there was a widely held view that the present distribution of living things could not be explained on the present distribution of land and sea, and that changes in this feature must be a potent factor in distribution.

For instance, Hooker (126) quotes Lyell as saying: "As a general rule, species common to many distant provinces, or those now found to inhabit many distant parts of the globe, are to be regarded as the most ancient . . . their wide diffusion shows that they have had a long time to spread themselves, and have been able to survive many important changes in Physical Geography."

Hooker (127) himself, in his *Introductory Essay to the Flora of Tasmania*, says: "These and a multitude of analogous facts have led to the study of two classes of agents, both of which may be reasonably supposed to have had a powerful effect in determining the distribution of plants; these are changes of climates, and changes in the relative position and elevation of land."

The final phrase of this statement of Hooker's is a particularly important one in that it distinguishes between the spatial relation of land surfaces, that is to say the distances between them, and their relief and outline, and it is important before going further to amplify this.

A study of a geological map of the world or of almost any particular continent or region will show that, generally speaking, sedimentary deposits are well distributed over it, and hence that these particular portions covered by such deposits must, at one time or another have been under water, with consequent modification of the outline and extent of the dry land. This alone is sufficient evidence that the present distribution and outline of sea and land has not always remained unchanged, and that there must at least have been considerable variations in level and elevation, either by movement of the land or by variations in sea level.

But this kind of change is not the only one which must be considered, and a far more important question is the extent to which the present relative position of the widely separated land surfaces of the globe has been maintained in the past.

Further, with regard to the first kind of change the study of geological maps also shows that in all the larger land masses of the earth there are large areas where very ancient Archaean rocks are exposed at the surface, and that in general these areas tend to be rather centrally placed. Furthermore, these ancient rocks normally extend widely beneath the sedimentary deposits already referred to. In fact it is justifiable to regard the continents and subcontinents as actually composed of a core or base of these Archaean formations, on parts of which from time to time sedimentary younger rocks have been deposited. These ancient rock surfaces, or Archaean shields as they are often called, are conspicuously noteworthy in Canada, in eastern South America, in Scandinavia, in India, in Manchuria, in Africa, in Arabia, in Madagascar and in Western Australia, but they are also represented on a smaller scale in many of the large islands.

There is also good geological reason for believing that all or nearly all of the superposed sediments are deposits formed under comparatively shallow water in which the Archaean base lay not far below the surface. On these evidences it is generally supposed that the sedimentary deposits of the larger land masses were formed during times when the peripheral parts of the land were for various reasons shallowly submerged.

These sediments vary enormously in age, and it is therefore unnecessary to assume that any land mass was submerged to the total extent of such deposits at any one time. Rather may we visualise the successive submergence of different parts of the continental edges in different periods, the various sediments being laid down in consonance with these submergences.

Approaching the matter from a rather different angle, we may therefore imagine that the seas around the masses encroached upon them locally and at various times according to changes in the relative elevation of land and water.

This conception immediately raises the question whether the present extent of the continents is a maximum one or whether in fact some parts of them are even now invaded by shallow seas. To put this also in rather a different way, the question is whether or not the present land outline of the continents actually represents the boundaries of their Archaean bases.

To answer this question it is necessary to consult a map showing the submarine relief. Here we shall at once notice that the shallower submarine contours closely follow the outline of the land, but that as depth increases so they become more irregular. This means in effect that round most land surfaces there is a narrow edging of very shallow water beyond which the sea becomes rapidly deeper. The details of this distribution leave no room for doubt that the line where the sea passes from shallow to deep represents the real edges of the continents, but that they are, in general, slightly encroached upon by the sea. These submerged edges of the continents are usually called continental shelves, and one of the most striking is in western Europe, where the real edge of the continent runs west of Ireland, so that the British Isles are to be regarded as islands rising out of the sea from the surface of the continental shelf which elsewhere forms the beds of the shallow seas which separate them from what is generally called the "continent."

Seas of this kind, which are clearly intrusions or encroachments over the land surfaces of the continents, are called epicontinental seas, and, by a justifiable extension of the phrase, sedimentary deposits formed on their beds may be called epicontinental deposits.

Although the case of Great Britain has been cited because of its obvious familiarity, it affords by no means the most extensive example of epicontinental

seas, and far greater extents of shallow waters which are presumably to be regarded as real epicontinental seas are to be seen in south-east Asia, where they extend over much of Malaya. Especially noteworthy is the occurrence of such shallow seas between Australia and New Guinea.

On the other hand, many parts of the world are conspicuously without these epicontinental seas, and here the shore edge is more or less exactly the real continental edge. The west coasts of Africa and America and of Australia are perhaps the best instances of this.

A point of considerable interest is whether or not we are to visualise the real edges of the continents as all at about the same level, or whether different continents are more deeply invaded by water than others. This is a very complicated point and one which can here only be answered somewhat obliquely.

If we return to our examination of submarine contours we shall notice that one of those most generally illustrated is the 200-metre or roughly the 600-ft. contour. There is no inherent virtue in this figure, and its constant use is based on the fact that it serves to reveal the salient points of underwater relief particularly vividly. In other words, it does generally mark the point at which a very gradual deepening of the sea becomes suddenly and intensely accentuated. On this account it is a reasonably fair inference to assume that it represents in general the depth to which epicontinental seas may attain in the present circumstances of the earth.

We may indeed be permitted to regard for our present purposes this 600-ft. submarine contour as giving a general if not an exact impression of the actual outlines of the main land masses of the globe.

This enables us to gain a much clearer picture of what changes in the relative levels of land and sea and particularly of what, to coin a rather ugly word, "epicontinentality" may mean, because by following this particular contour we can draw an outline of the continents as they would presumably appear if they were at their maximum elevation relative to the sea and if on this account they were free from the encroachment of epicontinental seas.

A map of this kind is most illuminating (Plate 3), and rather astonishing. It will already have been inferred that Great Britain would be joined to the continent, but this is only a very minor aspect of the whole. Taking the continents in order, we should see that in Europe there is not much other change except that the narrower straits of the Mediterranean disappear. That sea as a whole survives, though in slightly diminished size. In Africa, too, the only change of note is the joining of the Canaries to the mainland.

In America the changes are much more extensive. Working from north to south, the Arctic Archipelago would disappear and become a continuous extension of the northern mainland, and the North Atlantic would be almost bridged; Newfoundland would be united to Canada; the Bahamas and Cuba would be practically continuous not only with Florida but also with Yucatan; the rest of the West Indies would be much more extensive; and finally the Falklands would be connected up to Fuegia.

Extensive as these American changes would be, they are slight compared with what would have happened in eastern Asia and Australasia. Here, once more starting in the north, the Bering Strait would disappear; Japan and Sakhalin would be joined to the mainland; the Philippines, Borneo, Java and Sumatra would all be joined to the continent by way of the Malay Peninsula and Siam; and, finally, New Guinea would be joined to Australia.

From the point of view of plant distribution this means that with a few quite minor exceptions practically all the islands of the northern hemisphere would be replaced by continuous land surface, and the only discontinuity would be that of the ocean basins. Is it justifiable to assume that this condition has in fact existed during the history of flowering plants?

There are several lines of evidence which go to show that the present condition of affairs is not an extreme condition in either direction. The distribution of Tertiary epicontinental deposits shows clearly that the continents must, as a whole or in part, have been much more submerged than now at some period since the Angiosperms became widespread, and the same is true of earlier times, the great Cretaceous transgression in North America being a striking case in point. On the contrary, we know from direct evidence that they have also been much more elevated. For instance, at one time the British Isles are generally supposed not only to have been joined to the continent but also to one another. Evidences of elevation are also fairly convincing in mid-America. Both these would presumably involve changes of the magnitude required to produce the results described above, and there is certainly no reason to doubt that they may have occurred.

These changes, however, involve increase in land surface, and it is interesting to try to draw a picture of the other extreme and to see how they may have been restricted at certain periods. It is not at all easy to do this, but something of the sort can be done by tracing the outline of the continents as they would appear if those areas on which there are Tertiary or more recent deposits are excluded as if they were in fact beneath the sea. It would take too long to go through the whole world on this basis, but a further glance at a geological map will show in the case of Europe and Asia, for instance, the sort of degree of change that might be expected.

Great areas of north-east Siberia are covered with Tertiary deposits, as is also much of the interior of Asia. Similarly in Asia Minor and in Europe, and at least it can be said that a very appreciable proportion of the whole area might well have been simultaneously submerged at a time of maximum relative depression.

With the possible causes of the depressions and elevations we cannot concern ourselves here, but it may help to clarify the picture which is forming in the reader's mind to say that one view supposes that at the time of the maximum glaciation such quantities of water were locked up in the ice-sheets that the sea was distinctly lowered throughout the world. On the other hand, it is only fair to say that others suppose that the weight of these great ice-sheets may have had the opposite effect and may have depressed the continental level.

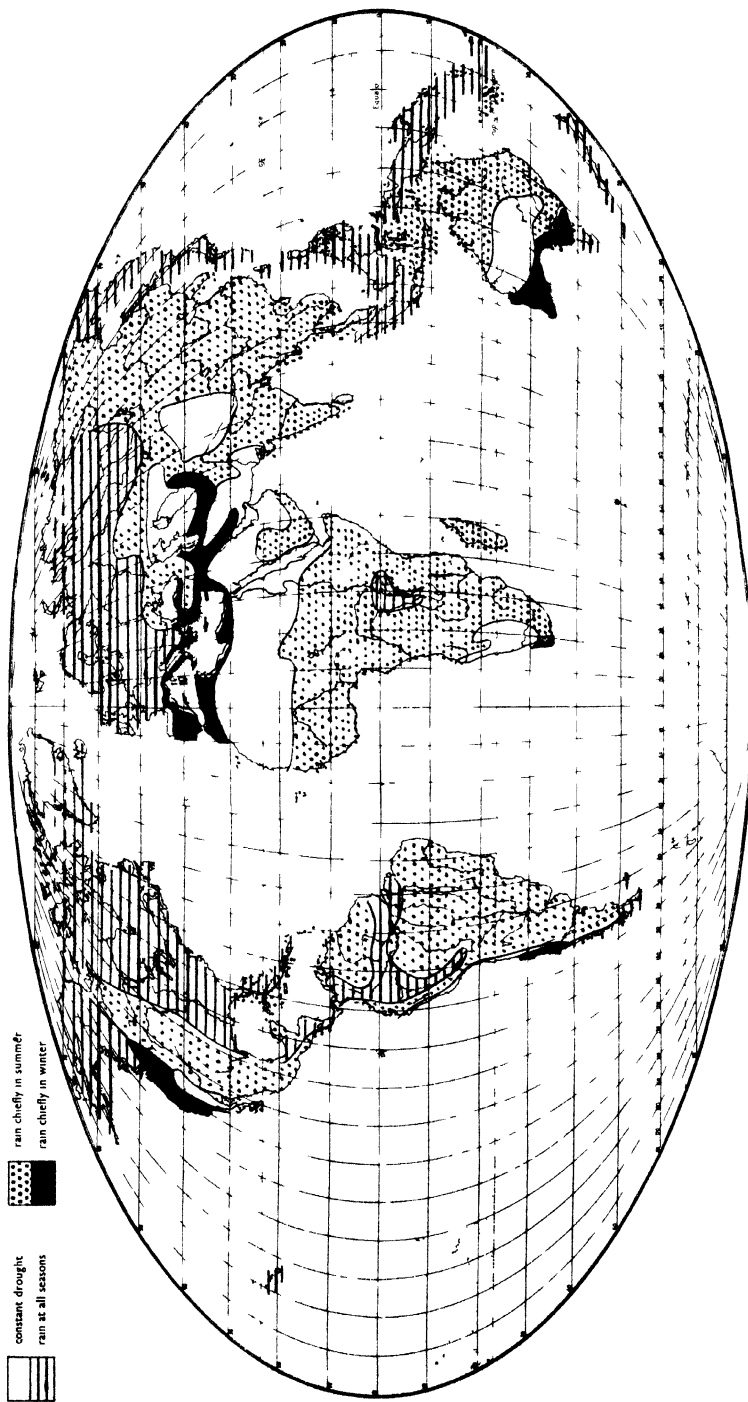
One of the most likely resolutions of this difficulty is that these changes in level are best to be regarded as due to tilting of the continental surfaces rather than to their absolute vertical movement. This view also has the advantage that it permits the conception of simultaneous elevation and depression in different parts of the world. That such tilting has occurred there is ample evidence, and that it may also have occurred very locally is shown by the study of the raised beaches round our own coasts, which suggest a tilting of Great Britain along a north-south axis at a comparatively recent date (194).

Certainly, whatever the actual details may have been, it is inevitable that we must think in terms of very considerable epicontinental changes during the history of the Flowering Plants, and, moreover, that these changes must at one time or another have affected the distribution of these plants in three ways. First, they must have controlled plant movement and dispersal by the formation or

Map of the World showing the seasonal distribution of rain. After Bartholomew's *Physical Atlas*, vol. III



PLATE 24



Areas correct Distortion increasing towards border of map
 Approx. scale 1:100,000,000 (600 miles inch along equator)
 on Mollweide Homographic Projection

elimination of barriers. Second, they must have led to tremendous changes in the actual amount of land available for plants. Third, they must have caused correspondingly great changes, not only in the zonation of climate, but also and as a consequence in the prevalence of habitat types.

So far we have argued on the tacit assumption that the size of the various land masses has remained the same but that their degree of exposure above the sea has varied. Let us see how far we are really justified in this assumption.

This question involves certain very abstruse aspects of geophysics, and the only reason for their mention here, especially by a botanist, is their exceptional interest from the point of view of the geography of plants in general and of this chapter in particular.

Perhaps the easiest way to approach them is from the subject of mountain building. The fact that certain geological epochs, and especially the Miocene, were periods of intense mountain elevation has already been referred to more than once. Mountain building on a large scale may be described as a corrugating of the earth's surface widely or locally according to its extent. This can be illustrated in a familiar way by compressing a flat surface like a sheet or pile of paper laterally. In so doing, however, not only is the surface thrown into folds but the ends of the paper are brought closer together, so that the horizontal distance between the ends is decreased. That such compression folding has indeed been the mode of formation of many mountain systems has been shown quite conclusively in the case of the Alps, for instance (48), where it appears that part of North Africa has actually been pushed into south Europe. The difference is that in the paper the folds are hollow while on the earth they are solid, and this means that matter must be found from somewhere to fill them. Hence mountain building must mean a great displacement of material and, to express the point in but one way, a thickening of the continent at the expense of its superficial area. On these quite general grounds it may be supposed that mountain building will lead to a contraction of surface.

Modern geophysics, however, goes even further than this, and it is at this point that our study becomes abstruse. It involves a conception which is known as isostasy. According to this—and it can be referred to here only in the most general terms—the increase of matter on the upper surface of the continents caused by the corrugations is matched and compensated for as it were on the under surface by a corresponding thickening.

In terms of isostasy, in short, we have to regard the formation of great mountain ranges as causing a redistribution of the materials of which the continents are composed even greater than might be expected at first sight, and the probability that such redistribution will be expressed in the size of the continental masses, namely their area, is thus enhanced. As regards this particular and immediate problem we need not go further than to conclude that there is then sound reason for supposing that the continents may have varied in absolute area in the past as well as in area inhabitable to land plants.

So far, however, we have been concerned only with the comparatively minor geographical changes which may have been brought about by the relative elevation or depression of the continents or by changes in their actual size. These, we have shown, may have been and indeed almost certainly have been considerable, but even so they are minor compared with the possible changes which may have taken place by alteration in the relative position of the continents. This much wider question must now be considered.

The very brief mention of isostasy above was made because it served two useful purposes. Not only was it apposite to the more restricted question there involved, but it was an essential introduction to the more general question of continental position now to be considered, in that it clearly indicates that what may be regarded as the normal and everyday ideas of continental structure and behaviour have, in the light of modern knowledge, to be radically revised.

To the ordinary man in the street a continent is symbolic of all that is solid, rigid and unchangeable, but the geophysicist has quite a different conception, because to him such attributes as solidity and rigidity have a different and more precise connotation. On his criteria very few kinds of matter merit these descriptions, and a continent is certainly not one of them. How then is it to be regarded?

The best way of explaining this difficult point is to pass straight into as simple an account as possible of the crust of the earth as it is believed to exist in the light of modern physical ideas.

In brief, the outer layers of the earth's core are pictured as being of the consistency of a very viscous liquid, "solid" by all ordinary standards but essentially fluid in the strictly scientific meaning of the term. On the outermost layer of this fluid core the continents, themselves more rigid though far from absolutely so, float partially immersed. The layer of the core in which they float is called the "sima," from the amount of silica and magnesia in its constitution, and the continental slabs themselves are called the "sial," from the amount of silica and alumina which they contain (fig. 70). The continental slabs vary in thickness, superimposed matter due to mountains on the upper surface being accompanied by a corresponding increased thickness on the under surface according to the principles of isostasy. Between the continents, that is to say over the beds of the oceans, the surface of the sima is in direct contact with the water. To summarise these modern conceptions, the continents are pictured as isolated slabs of one sort of material floating partially immersed in another sort of material.

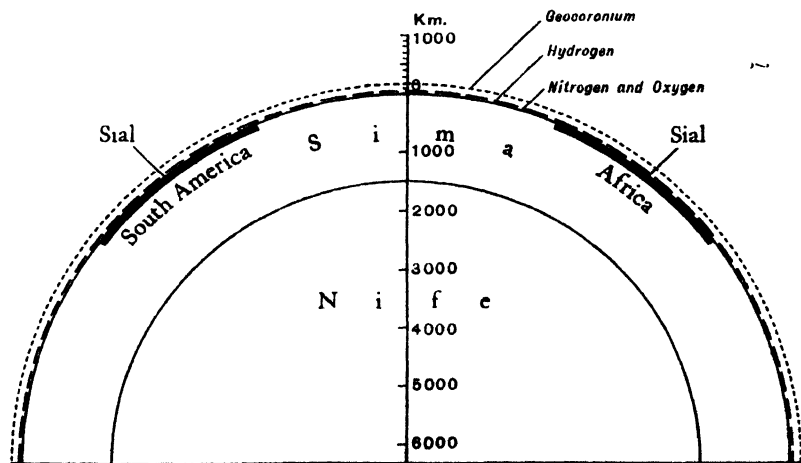


FIG. 70.—Diagram of a section of one hemisphere to show the position of the sial and sima. (Redrawn from Wegener, *Origin of Continents and Oceans*, Methuen & Co.)

With this picture before us we shall at least be partially equipped for an investigation into what is one of the most topical of all subjects to-day—the question of whether or not the continents have always been in the relative positions which they at present occupy.

There seems little doubt that the idea of continental movement, or drift as it is now more generally called, has been vaguely in the minds of men for many years, but the whole conception is so revolutionary and so opposed to traditional teaching that not until this century was it put forward as a definite hypothesis. Even so the first attempts to do so were tentative, and it was not until Wegener (257) published his book *Die Entstehung der Kontinente und Ozeane*, in 1915, that the theory came into full prominence. Because Wegener's presentation of his views was the first really illustrative attempt to put continental drift into words, the ideas enshrined in his book as well as his name have become rather too intimately linked with the general theory, and it should be remembered that he was but one of a number of apostles.

The theory is as follows. During the earlier part of the Palaeozoic epoch the continents of the world were all joined together into one huge land mass or Pangaea, and subsequently they separated and drifted apart until they have come to reach the positions they now occupy (fig. 71). This movement centred on Africa, which, with the main part of continental Asia, has retained its original position more or less unchanged. The theory also envisages a movement or wandering of the poles, thus accounting for considerable alterations in the distribution of the climatic zones.

Since the publication of Wegener's book the theory of continental drift has received a great amount of attention (e.g. 277, 285) and many improved forms of the theory, correcting or modifying some of the more obvious weaknesses of Wegener's ideas, have been elaborated. Fortunately Du Toit (67) has brought together in one volume much of the relevant matter relating to such theories, to which he has added many of his own ideas, and to this work the writer is indebted for much of the following discussion.

It would be out of place to consider here the many very controversial aspects of the subject, but it is essential to survey very shortly the evidences on which the idea of drift is based. These Du Toit has most usefully summarised as the "criteria of drift," and a much simplified presentation of them is as follows:

1. Physiographic:

The general similarity in shape of many opposed coast-lines such, for instance, as those of eastern South America and western Africa.

The correspondence of physiographical features in lands now widely separated.
The occurrence of various submarine features producible by drifting blocks.

2. Stratigraphical:

The occurrence of similar geological formations on opposite coasts.
Other geological resemblances on separate masses.

3. Tectonic:

The occurrence of comparable geosynclines, fold systems, fault systems and rift valleys on different continental masses.

4. Volcanic:

Similarities between the volcanic geology of separated masses.

5. Palaeoclimatic:

The peculiar distribution of glacial deposits and of other extreme climatic types of deposit over the different continents.

6. Palaeontological :

These may be comprehended in the single statement of the difficulty or impossibility of accounting for the present distribution of organisms on the assumption that the major distribution of land surfaces has been constant. It involves in detail a great many important special aspects such, for instance, as the floral relationships between America and Africa and between the widely sundered lands of the southern hemisphere. The distribution of marine organisms also presents many very difficult problems on such an assumption.

7. Geodetic :

This may be interpreted as the evidence afforded by the actual measurements of longitudinal and latitudinal values.

For further details of these criteria the works of the two authors cited should be studied, and it may be well to say here that while they show considerable differences in detail there are no essential discrepancies between them. For instance, there are differences of opinion about the course of continental drift and also about the condition of the world at the time that it began (Du Toit postulates two primaeval continents, one northern and one southern), but these do not affect the general theory.

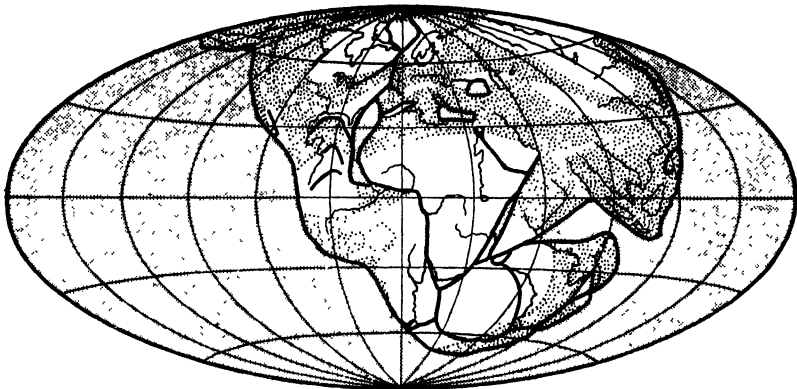
The last two of the above criteria need, however, further reference here. Let us dispose of the latter first. It is particularly important here, because to those who are not expert geologists or geophysicists it is by far the most easily understood evidence, and even to them it must be the most conclusive. In short, has actual astronomical and mathematical measurement shown that the continents have moved or has it not ? The matter is considered at length by Du Toit, and, as it is one of great complexity and controversy, it must suffice to quote here his conclusions, which are " it must therefore be concluded that a positive shift of crustal matter has been instrumentally demonstrated."

The details chiefly concern areas in the higher northern latitudes like Greenland, and the actual extent of movement is no more than can be measured in yards, but that it does exist and that these areas are slowly changing position seems reasonably certain although there is not yet complete agreement on the matter.

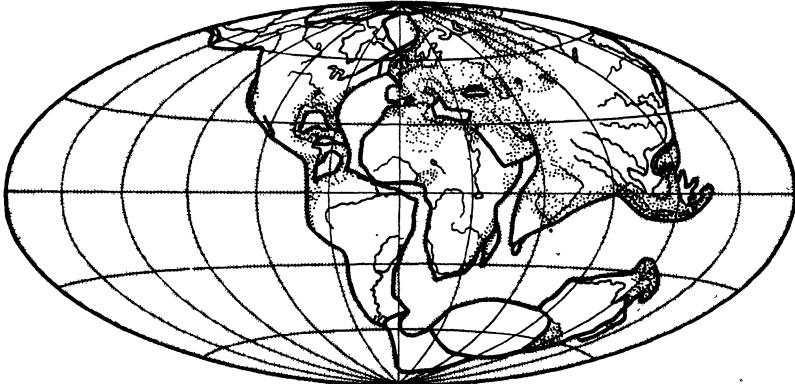
The evidence based on the distribution of organisms, and especially of plants, is clearly one which is of peculiar relevancy here. To review it at this point would necessitate repeating much of what has already been said in earlier chapters, and especially in those pages dealing with discontinuity. The theoretical importance of that aspect of plant geography has been emphasised more than once, and that importance is largely in relation to this question of continental drift. As illustrating the nature of the evidence it is only necessary to draw the reader's attention again to the lists of generic discontinuities in Chapter 6 and Appendix B.

Unanimity in scientific questions is very unusual, but it is probably no exaggeration to say that the opinion of plant geographers is almost unanimous that the present distribution of plants cannot be explained without allowing for some kind of alteration in the distribution of land and sea—that is to say, without assuming that the now severed continents have been joined to one another at some time in the past.

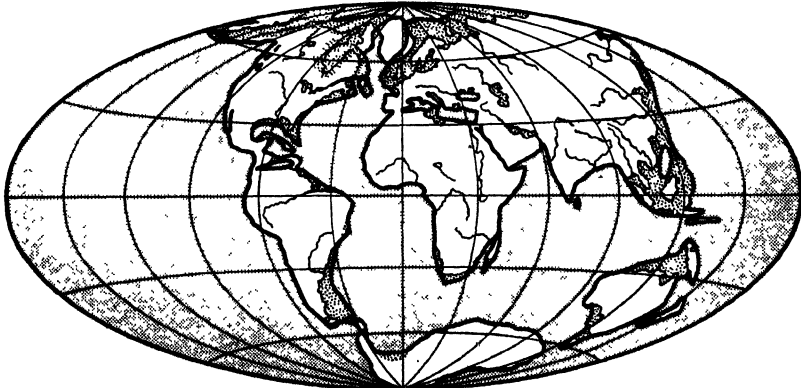
At first sight this might be interpreted as an acceptance of the theory of continental displacement, but this is not so. There is an alternative, and it is this alternative which up to now has held the field. Two methods are obviously possible by which separated units may be joined. One is by the movement of one



Upper Carboniferous



Eocene



Older Quaternary

FIG. 71.—Reconstruction of the map of the world at different periods in geological history, according to Wegener's theory of continental displacement.
(Redrawn from Wegener, *Origin of Continents and Oceans*, Methuen & Co.)

or both towards one another. That, in terms of continents, is the theory of continental drift.

A similar but less direct effect can be obtained by leaving the units where they are and bridging, by some means, the gap between them. This, in terms of continents, is the theory of land bridges, which in the past has been held almost universally.

From the point of view of this book then the problem of continental drift narrows itself to this more particular problem of how the present discontinuity of the continents has been brought about, and, as a corollary, in what way they were originally joined. This question has already been discussed at some length by the writer in relation to the genus *Coriaria* (95), and it is relevant to say that he has found no reasons to revise, in the years which have passed since its publication, what was there said. More recently Seward and Conway (217) have also made some important comments on the theory.

It is interesting to note that the land bridge theory is in worse plight than the drift theory, in that there is not even a modicum of direct evidence for it. There are no unmistakable traces of extensive former land surfaces now sunk beneath the sea, as the theory must envisage. How then did the theory arise? The answer is that it must essentially have originated as a theory *faute de mieux*—that is to say, as the only conceivable explanation. But this clearly makes the criterion of it largely that of what can or cannot readily be conceived by the human intelligence. Until the coming of the idea of evolution human thought in general and scientific thought in particular were bounded by conceptions of cosmogony of so ponderous a traditional weight that only the most exceptional intelligences could become free of them. It is therefore not surprising that the possibility of continental movement did not enter the mind, and in the absence the theory of land bridges was inevitable.

Unfortunately these circumstances gave to the theory of land bridges a long and complete freedom from question, and it was established so firmly that its overthrow became exceedingly difficult, though by no merits of the theory itself. Indeed it is in many respects a very weak theory and there is much evidence against it. The nature of this evidence has been discussed in the papers mentioned above, and we can only summarise them here in a very general way.

The occurrence of marine deposits on what is now land, and the occurrence of land or freshwater deposits where there is now sea, might be likely to afford at first sight evidence of bridges or at least of the sort of geographical changes that would produce them. The earlier part of this chapter has sufficiently shown, however, that the first have been produced by epicontinental seas and have no relation to the actual shapes and areas of the continents. The second, it is very interesting to note, are apparently not known at all. Wherever there are deep oceans their floors are either bare or covered with abyssal deposits such as oozes.

The next salient fact is that none of the oceanic islands now to be found along the lines of supposed former land bridges contain any sedimentary deposits such as those so characteristic of continents and of which their vestiges would be likely to consist. More than this, such islands are either volcanic islands, often of very recent date, or they are no more than coral atolls. It is apparently true to say that in practically no case does the structure of an oceanic island suggest that it is the remnant of a continental mass which has subsided.

This very phrase is significant, because, if continental movement is to be rigidly excluded, then only subsidence or some unimaginable catastrophe can explain the

disappearance of the hypothetical land bridges, and to suppose that huge land areas can be "versunken ohne Spur" strains the imagination.

So much for what may be called the unlikelihood of land bridges, but the actual idea is very much less promising than would appear at first sight. In the first place, the phytogeographical problems which land bridges particularly are called to explain are mostly those of Angiosperms, and hence any land bridges envisaged must date from the Cretaceous or later. Again, the list of discontinuous genera in Appendix B is sufficient to show that in the period elapsed since the Cretaceous it would be necessary to postulate land bridges in practically every direction, between America and Africa, between Africa and Asia, linking the scattered lands of the south, joining up all oceanic islands with some mainland, and extending right across the Pacific. In short, it is necessary practically to cover the world with bridges, and, moreover, more or less simultaneously. Such an assumption is unwarrantable, and it is no small point in favour of continental drift that it avoids the necessity of relatively enormous increases in the land areas of the globe, to which most geophysical arguments are opposed.

It must not be supposed from this that no land bridges can have existed in any circumstances or time, nor that faith in them has been entirely abandoned (103, 104). It has already been shown that comparatively small elevations would serve to link up what are now quite widely separated areas. But land bridges are tacitly meant to be land areas crossing the main ocean beds, and for such it can only be said that the evidence is in no case adequate.

It is fair to say that many of these difficulties are realised and attempts have been made to meet them, and that few geologists would be prepared to accept the bare land bridge theory without saving clauses. For instance, one view supposes that there was in the Palaeozoic a huge mainly southern continent (Gondwanaland), and that this, to use the current phrase, "broke up" in the Mesozoic. The breaking up is visualised as a differential sinking of its constituent parts so as to produce a discontinuous series of land masses. The interesting point about this is that it takes liberties with the stability of continents such as are so often disallowed to the protagonists of drift.

Land bridges are far from being the universal remedy that they appear, for other reasons. One in particular is that the submergence of great extents of land will not necessarily produce the phytogeographical effects actually to be observed. For instance, very wide discontinuity of types will follow only if those types were completely distributed throughout the bridge and, incidentally, in very constant form. Otherwise the subsidence of the bridge would have to take the most peculiar and special course to produce the observed discontinuity.

As a matter of fact these difficulties have been realised often enough and frequently, be it noted, by those who rank as foremost among authorities on distribution. Wallace (251), for instance, believed firmly in what he called the permanence of continents and would not admit the possibility of land bridges. He was thus faced with the necessity of explaining discontinuity largely on the basis of dispersal, and this, to say the least, is a very uneasy standpoint.

Turning now once more to the theory of continental drift, it is not unfair to say that many of the criteria mentioned by Du Toit—that is to say, the indirect evidences of the theory—are very compelling. It would be presumptuous to make further comment on the inorganic side of the question, but it is permissible to refer once more to the evidences afforded by plant distribution. On this point it can be said, in the writer's opinion without fear of rebuttal, that the theory of

continental drift explains the peculiarities of distribution to a degree of completeness far beyond that of any other theory. By this is meant that not only is drift more likely than bridging on the phytogeographical evidence, but drift can explain the details and the sequence of distribution in a way quite beyond the power of the theory of land bridges or the theory of distribution entirely by dispersal. The writer also believes that no one can read the earlier chapters of this book dispassionately without coming to the same conclusion.

But if this is so, why is the theory of drift not more widely accepted than it is? The answer to this very reasonable enquiry is that there are three important objections to it. Important, yes, but it is interesting to note that each is peculiarly unsatisfactory. The first is the purely psychological objection to something which not only breaks entirely new ground but which in doing so causes an upheaval among long-established institutions. If the theory of drift is true, then a vast amount of what has been written on all sorts of topics is untrue, and, since many of the authors are still able to defend their works, there is an enormous inertia against the theory. Du Toit has expressed this so vividly (the italics are his) that we cannot do better than quote his words, in which he says:

" . . . it must frankly be recognized that the principles advocated by the supporters of Continental Drift form generally the antithesis of those currently held. *The differences between the two doctrines are indeed fundamental and the acceptance of the one must largely exclude the other.* Indeed, under the new hypothesis certain geological concepts come to acquire a new significance amounting in a few cases to a complete inversion of principles, and the inquirer will find it necessary to re-orient his ideas. For the first time he will get glimpses—albeit imperfect as yet—of a pulsating restless earth, all parts of which are in greater or less degree of movement in respect to the axis of rotation, having been so, moreover, throughout geological time. He will have to leave behind him—perhaps reluctantly—the dumbfounding spectacle of the present continental masses, firmly anchored to a plastic foundation yet remaining fixed in space; set thousands of kilometres apart, it may be, yet behaving in almost identical fashion from epoch to epoch and stage to stage like soldiers at drill; widely stretched in some quarters at various times and astoundingly compressed in others, yet retaining their general shapes, positions and orientations; remote from one another throughout history, yet showing in their fossil remains common or allied forms of terrestrial life; possessed during certain epochs of climates that may have ranged from glacial to torrid or pluvial to arid, though contrary to meteorological principles when their existing geographical positions are considered—to mention but a few such paradoxes!"

This extract illustrates a point which it is desirable to stress, namely that the conceptions of continental structure described in the earlier part of this chapter, such as the sial and the sima, continental floating blocks and isostasy, are not particular or peculiar features of the theory of continental drift. They are rather quite generally accepted views on modern geomorphology. That they are so apposite in view of possible drift is then distinctly in favour of that theory.

This point is seen to emerge in an interesting way from the consideration of the other general objections to the theory of drift. The second and the only one which approaches the scientific is that there is not known any force which could possibly be regarded as sufficient to move the continents in the way suggested. That is to say, there is no satisfactory explanation of their movements. This objection has all too often been accepted as final, but it must be realised that at

best it is only negative. It would surely be untenable to suppose that there *cannot* be any such force. It simply is that no such force is at present known. The ordinary observer is not likely to be much impressed by such negative evidence, and besides it has been pointed out (191) most appropriately that this is exactly the position also with certain other geological beliefs which are generally accepted on their circumstantial evidence, as, for instance, the sinking of land bridges and the past Ice Ages. There is no reasonable known physical explanation of them either.

The third objection or series of objections is based on imperfections in the presentation of the theory by the earlier writers, and especially by Wegener. He, for instance, painted much too detailed a picture for the existing state of the theory, and thereby laid himself and it open to criticism on matters of really unimportant detail. No one even among the most fervent advocates of drift is prepared to accept the theory in the verbal form of Wegener, but it is obviously ridiculous to interpret this as evidence against the theory in general. Wegener, for instance, made his chronology so definite that it is easy to pick holes in it, but this has no real bearing on the likelihood or the reverse of drift. Again, he postulated displacement of the poles, and in doing so in so many words gave his adversaries a useful weapon, since there are powerful arguments against this conception. More recent writers have expressed the matter in terms of permanence of polar position but creep of the earth's crust relative to that position, and this apparently satisfies the critics! The effect, of course, is the same.

There is no doubt that many who have felt themselves unable to accept drift have nevertheless realised the weakness of their position and have put forward views to rationalise it. There is space for reference to only one of these, which seems to the writer to be particularly significant from the point of view of plant geography. This is the Theory of Climatic Cycles of Joly.

Joly (138) supposed that in the course of time the internal heat of the earth accumulates as a result of radioactivity, and that the effect of this is to melt the sima progressively outwards till that layer supporting the continents and oceans becomes molten. At this stage the heat of the earth becomes rapidly conducted away by the oceans and the continents, so that the earth becomes rapidly cooler again and resolidifies, to begin the cycle once more.

This theory was propounded to account for certain major features of geological history, and especially for the observed repeated but long-separated periods of climatic catastrophe (glaciation), epicontinentality and mountain building. Joly by the theory supposed that these are the inevitable consequences of the stages at which the outer layer of the sima becomes molten. Strangely enough, Joly did not admit the possibility of continental movement to any degree in these circumstances, despite the fact that they might on general grounds be supposed to be exactly the conditions to favour it.

This is mentioned here simply to illustrate two very important points. First is the very anomalous position in which many of the opponents of drift inevitably find themselves, in the light of their own opinions on related topics. The second is the writer's belief that Joly's theory contains the germ of the particular form of the drift theory especially indicated by the facts of plant geography, a view already expressed by Bews (25), who looks forward to a combination of the views of Wegener and Joly.

Generally speaking, theories of continental drift envisage more or less constant movement of land masses over very long geological periods of time. Wegener,

for instance, made his displacement begin in the Carboniferous and continue till to-day, and other writers do not diverge far from this position. This is not altogether in consonance with what we know of the history of Angiosperms. We have seen that this history seems to have consisted largely of two phases: first, a very long one covering the later Cretaceous and most of the Tertiary, and characterised by constancy and geniality of climate and by floristic generalisation; and, second, a much shorter period of upheaval, climatic, edaphic and floristic.

The world-wide constancy and dominance of the Angiosperms seems to indicate that such differentiating factors as geological isolation played but a small part during their early stages of development. That they may have done so to some degree is suggested by the appreciable distinction into northern and southern Angiosperm types, especially among what we regard as the older ones, and it is significant that this falls well into line with Du Toit's conception of two primaevae continents. The marked specialisation and geographical restriction of types which we must regard as relatively young, such especially as the semi-xerophytic herbs or undershrubs, suggests, on the other hand, that the appreciable isolation which has assisted that specialisation must have been recent, and also perhaps progressive.

Accepting as premises these facts and indications of Angiosperm history, then the botanical evidence seems to require that drift shall not have been marked or continuous till well on in the Tertiary. The agreement of Joly's theory with this view is obvious, and if it permitted the conception of continental displacement or drift as a consequence of one of the cyclical revolutions described, it would provide what seems to be the ideal geomorphic theory from the point of view of plant distribution.

In short, the theory of continental drift would explain plant distribution to-day to a most remarkably complete degree if it could be postulated in the following terms and be made to incorporate the following points:

1. That at least between the Cretaceous and the middle or later Tertiary the continents were, more or less, joined into one and were fixed in position.
2. That as a consequence of the thermal reaction pictured by Joly the sima became molten in the latter part of the Tertiary.
3. That continental drift resulted, first at a rapid rate and later, as the sima cooled, more slowly.
4. That an immediate consequence of this drifting was the uplifting of mountain ranges on the forward sides of the moving masses.
5. That a later consequence of the rapid loss of heat was the oncoming of the glaciations of the Pleistocene.

If, as is said, a theory incorporating these points could be put forward, then it would not only explain most points of plant geography but would also picture the main outlines of the sequence of events by which the Angiosperms have attained their present development in various parts of the world. Each point in the above summary is provided for by one view or another. If these possibly divergent details could be synthesised into a whole, it would be an almost entirely satisfactory phylogenetic theory of plant distribution.

To conclude a chapter which has taken us in places far away from plant geography, let us try to summarise the position as it appears to be to-day.

1. Many features in the present distribution of plants, and especially those associated with wide discontinuity, cannot easily be explained.

2. Three general explanations are possible :

a. That they are due solely to dispersal factors.

b. That the now separated continents were once joined by bridges.

c. That the continents have changed their relative positions.

3. All three of these have probably acted to some extent, and the question is one of deciding which has been of paramount importance.

4. The inadequacy of dispersal has been demonstrated in Chapter 18.

5. There are grave objections to the view that land bridges are the main cause.

6. The conception of continental drift affords a satisfactory explanation, but the theory is not yet universally accepted.

7. The various objections to the theory of continental drift are gradually being resolved and there is every reasonable prospect that the theory will, in its final form, not only receive general support but will provide the desired explanation of many problems of plant geography.

CHAPTER 21

THE THEORY OF TOLERANCE

IN the last six chapters the factors of distribution were first reviewed in general and then discussed in particular. The purpose of this chapter is to consider how far and in what manner they can be made to provide a theoretical explanation of the geography of the Flowering Plants.

What has already been said makes it clear that there are certain general statements which can be made regarding the causes of plant distribution, and that these are so incontestable that they may rank as general principles of plant geography. These principles are fundamentally six and may be expressed most concisely as follows :

1. Plant distribution is primarily controlled by the distribution of climatic conditions (see Plates 2, 4 and 5).
2. Plant distribution is secondarily controlled by the distribution of edaphic factors.
3. Great movements of species and of floras have taken place in the past and are apparently still continuing.
4. Plant movement, especially in its larger aspect of plant migration, is brought about by the transport of individual plants during their dispersal phases.
5. There has been great variation and oscillation in climate, especially at higher latitudes, since Angiosperms became prominent.
6. At least some, and probably considerable, variation has occurred during the same period in the relative distribution and outline of land and sea.

Although in the light of what has been said earlier these principles need no further demonstration, there are one or two points connected with them which have not yet been adequately noted. The first is the relation between the first two principles. The facts of plant geography everywhere show that the first of these is the more fundamental and that plant distribution is basically a climatic distribution. Edaphic factors can have but a secondary rôle, if for no other reasons than that they themselves are often controlled by climatic considerations. Moreover, edaphic factors tend to be distributed without much regard to latitude, whereas plants are normally correlated in range with latitude unless the factor of altitude, which is itself a climatic effect, comes into play.

Actually the difference between the two factors is best expressed by saying that while climatic factors control the extent of distribution, edaphic factors control its intensity. On climatic factors will depend whether a given species shall be a potential occupant of a given area ; on edaphic factors will depend whether it will in fact occupy it, and if so in what relative abundance. Climatic factors must decide whether an area is open to colonisation by a species in view of its general atmospheric requirements ; its eventual presence will depend on whether or not there are habitats suitable for it. Usually the more numerous and larger such habitats are, the more plentiful within this area will the species be. Naturally other factors may also be involved, but this is a fair general statement.

Except for the third, each of the six principles comprehends one of the

main factors of distribution already discussed at length, and one of the most important points is that they and the factors involved in them are of two kinds.

The first two and the fourth can be distinguished from the rest as being *internal*, in the sense that they concern the inherent constitution of the plant. In the first two the aspect of constitution concerned is the physiological, and in the fourth it is the structural.

Numbers five and six are *external* or extraneous, in the sense that they are no more than guides controlling the direction of effects resulting from the inherent conditions of plants.

The relationships between the six principles are fairly clear and generally accepted. That between the first two has just been dealt with; that between the third and fifth is believed to be one of effect and cause; the fourth explains the mechanism of the third; and the sixth will control to a greater or lesser extent the result of the third.

Indeed, taking the whole six principles together, they clearly indicate what is in effect a theoretical explanation of plant distribution, namely that it is the result of complicated plant movement or migration under the influence of climatic change, this movement being achieved by dispersal and being modified by contemporary topography, and this, with or without minor modification, is the view generally held to-day by those who are familiar with the facts and history of plant geography.

At first sight this view, which is at least one hundred years old and which may be called for convenience the Theory of Climatic Migrations, appears to be all that is to be desired, but on close examination it will be seen to be deficient in one very important and fundamental respect. It visualises plant movement; it indicates exactly how such movement may be made; it indicates the primary cause of such movement, but what it does not do is to explain why the cause (climatic change) should actually result in the movement or migration of plants. How the result can be achieved is clear, namely by dispersal. As to *why* the cause should have this particular result there is no indication. There is no conception of how and why climatic change is able to bring about plant movement by the agencies of dispersal.

As it stands the theory is like a locomotive which lacks connecting rods. Climatic change may be compared with the steam power generated in the boiler, and plant movement, by means of dispersal, may be compared with the mechanical movement of the locomotive by means of its wheels, but just as without the connecting rods the first cannot be converted into the second, so the theory cannot be made to explain plant movement without some definite provision which, as expressed above, it lacks.

This deficiency is met by the tacit and therefore to such extent unsatisfactory assumption of what is in fact the conception of specific tolerance, namely the view that each and every species can exist only within a given range of external conditions, and that this tolerance to environmental values does not and cannot change so rapidly as to "adapt" itself to change in external conditions. On this assumption the species can only survive in so far as its dispersal methods are able to keep pace with the changing external conditions in such a way that its range is always that of the conditions which it requires for its development. On this assumption the necessary connecting rod is provided in the form of a rigid relation between the species and the conditions under which it can exist. This relationship prevents

the species from staying where it is and modifying its existence to the new surroundings which the movement of climatic values (climatic change) has brought about.

Let it be said at once that no criticism of this assumption on the score of its probability is possible. It may be that in the early days of the Flowering Plants climatic changes were so slow and gradual that species were able to adapt themselves to them by the processes of evolution, but at any rate in more recent times climatic changes have been so rapid and so drastic as to make this suggestion in general quite untenable, and it is to these rapid and recent changes that are undoubtedly to be attributed the major features of plant distribution to-day. The point at issue is that this all-essential part of the Theory of Climatic Migrations has grown up without proper presentation and without the standing which would be its due as a properly expressed and tested hypothesis.

To remedy this deficiency the present writer published some years ago a paper reconsidering the conception of tolerance and expressing it in the form of a definite theory (96). In that paper the six principles enumerated above were first dealt with, and there was then enunciated a Theory of Tolerance in the following terms:

"Each and every plant species is able to exist and reproduce successfully only within a definite range of climatic and edaphic conditions. This range represents the tolerance of the species to external conditions.

The tolerance of a species is a specific character subject to the laws and processes of organic evolution in the same way as its morphological characters, but the two are not necessarily linked.

Change in tolerance may or may not be accompanied by morphological change, and morphological change may or may not be accompanied by change in tolerance.

Morphologically similar species may show wide differences in tolerance, and species with similar tolerance may show very little morphological similarity.

The relative distribution of species with similar ranges of tolerance is finally determined by the result of the competition between them.

The tolerance of any larger taxonomic unit is the sum of the tolerances of its constituent species."

This enunciation was followed by a long discussion of the meaning and application of the theory, and, if for no other reason than that they serve to illustrate many points of general interest to the student of plant geography, the main features of this discussion may appropriately be summarised here.

According to the theory there must be a total area which a species can, in virtue of its tolerance, occupy, and this may be termed its "potential area." Its ability to cover this area depends first upon its dispersal over the area and then upon the result of the competition it may encounter in the process. If the potential area is large, competition will tend to vary in intensity in different parts of it so that establishment will not be equally easy everywhere. A species never can or will become established outside the potential area, and the size and position of the potential area will tend to vary with change in external conditions.

If tolerance is a specific character amenable to the laws of evolution and genetics, it may change in the same manner and from the same causes as structural characters, and since these latter are normally more or less closely correlated with conditions of life, some distinct relation between morphology and tolerance may normally be expected.

It is important to note that the theory as a whole visualises three kinds of change, each with its own particular speed. First, there is the rate of evolutionary change; secondly, there is the speed of change in external conditions; and, thirdly, there is the speed of movement of the species by means of dispersal.

It is a fundamental postulate of the theory that the first speed (evolutionary) is usually immeasurably slower than the other two, and that these (external change and dispersal) are normally comparable.

The tolerance of a species will be composed of many ranges of tolerance to individual conditions, but in practice one of these will usually become a distributional limiting factor. A narrow range of tolerance as regards one condition—say, for instance, rainfall—will control the distribution even though the tolerance to other conditions, perhaps to soil constitution, is much wider.

If tolerance to a particular condition or factor is so wide as to include the whole existing world gamut of this factor, the tolerance may be described as complete in respect of it. In the theoretically conceivable case of a species exhibiting complete tolerance to all factors and conditions, its potential area will also be complete, namely cosmopolitan, but there are no species which can be cited as possible examples of this.

The world gamut of most external conditions is relatively small, and, taking into account the great number of plant species, it must be presumed that many species will tend to have very similar tolerances, especially as regards one or a few factors. This is in accord with the observed facts of competition and affords a possible explanation of it. The result may be anything from the complete supremacy of one species to a balanced deadlock between two or more.

Many detailed studies in plant distribution (100) suggest strongly that within any range of tolerance as a whole there are minimum, optimum and maximum conditions. Existence, in absence of competition, will be possible within the whole range, but the species will only be at its strongest, in relation to competition and also to vigour, within certain optimum figures. It also seems certain that minute differences in tolerance between species, such as are imperceptible to the ordinary human observer, may be quite critical and decisive in determining the issue of competition. Conversely, very minute differences in external conditions may be vital to the plant.

The assertion that the tolerance of a larger unit is the sum of the tolerances of its constituent species needs no elaboration except to point out that these specific tolerances need not form a continuous range of values for any or all factors. Thus the tolerances of the species of a genus towards temperature, for instance, may have wide limits but they may not cover all values between these limits. As there is usually continuous variation in climatic values, this may well lead to the potential area of the genus being discontinuous, that is to say composed of spatially separated parts. This obviously has a direct bearing on the subject of discontinuous distribution, and is only one example of the way in which the conception of tolerance impinges on all sorts of geographical problems.

It may be added here that the corollary to this final phrase of the theory is that the tolerance of a species will, in its turn, be made up of the tolerances of its constituent individuals, since (as the third sentence of the theory states) these individuals may be variable in tolerance and in form.

The Theory of Tolerance bears also on the conception of Age and Area (see Chapter 3). A species or genus may be very restricted in range for one or other

of two totally distinct reasons. It may be because the unit has such a tolerance that the area occupied is in fact its whole potential area, in which case it is in at least a temporary state of equilibrium, or it may be because the unit has not succeeded in occupying more than a part of its potential area. Lack of time must always be a probable explanation of this, and thus area may be a matter of age, but only in certain circumstances. For instance, where a potential area is discontinuous, failure to occupy it may be attributable to such difficulties as those of crossing the space between the parts of the area, and this may have little or no relation to age, except that the longer a species exists the greater the chances of a successful crossing. Where the range of a unit is complete, that is to say where the whole of the potential area is occupied, area obviously can give no indication of age. It is practically impossible to say which of these circumstances prevails in any given case, and hence from the point of view of tolerance there seems little hope of deducing age from area.

It must always be remembered that change in external conditions is independent of change in tolerance except in so far as the latter is the result of the former. Hence potential area must not be regarded as something fixed but as something that fluctuates according to the distribution of external conditions. Supposing, for instance, that a species is able to exist only within certain precipitation values, its potential area at any time will be the area over which these values pertain. This clearly will vary in one way or another with the passage of time. This is no doubt a partial explanation of the well-known cases where a genus is known to have had in former geological periods a range much greater than it has to-day. Both the former extensive and the recent restricted areas may represent its potential area at the respective times. To this, of course, must be added the possibility that the constitution of the genus has altered by the extinction of species.

These are some of the points which arise in the consideration of tolerance, and there must now be considered exactly how tolerance works, that is to say, exactly how it makes movement inevitable if the species is to survive.

Imagine a species which is tolerant to a range of mean annual temperatures between 50° and 55° F. (the figure is purely illustrative), and suppose that the area over which these figures prevail, that is to say the potential area of the species, is continuous. Also suppose that its distribution is complete and that the range of the plant and the range of these temperature values are the same.

Every generation, if the species is monocarpic, and every reproductive season if the species is perennial, the individuals composing it will produce dispersal units (usually seeds or fruits), and these will tend to be disseminated in all directions from the parent plants. Except along the edges of the species area, dispersal, unless very wide, will cause the units to come to rest at a point within the existing area of the species. Along the edges of the area, however, the result will be different, since, if dispersal is in all directions from the parents, some at least of the dispersal units from the outer individuals will fall beyond the specific limits, that is to say outside their necessary temperature conditions, and will therefore be unable to develop successfully. This process will continue at reproductive intervals of time as long as the specific tolerance and the distribution of temperature remain unchanged, some disseminules each time failing to develop.

Now suppose that a climatic change associated with general lowering of temperature begins. Other things (such as topography) being equal, the temperature



Plate 25. Palms in Lower California

(from Karsten & Schenck, Vegetationsbilder)

area of 50°–55° F. will move towards the equator. What will be the effects on the individuals of the species? On the northern edge of their area there will be, as climatic movement begins, the equivalent of a contraction of potential area so that some of the disseminules, not only of the outermost plants but also of those slightly further in, will fall outside the necessary conditions. Before very long the parents which were originally the outermost will be themselves outside the potential area and will therefore perish. As the climatic movement continues the belt of destruction in its wake will widen.

On the southern edge of the specific area the circumstances will be exactly reversed. After a time none of the disseminules of the outermost individuals will any longer fall outside the potential area, but within it, and will mature successfully, producing disseminules in their turn. These new parents will at first disseminate themselves partly outside the area, but very soon, with the continuance of climatic change, their disseminules, too, will fall within the necessary conditions, and this process will be repeated in succeeding generations.

The combined effect on the southern and northern edges of distribution, together with the similar but modified effects on other parts of the periphery, will in fact be such that correlation is maintained between climatic and specific area, and hence, since the former moves, so also does the latter.

But this movement will only result if tolerance remains unchanged while climate alters. This is the most crucial part of the whole theory, and the reason for the comparison, in the enunciation, of tolerance and morphology in relation to evolution. It is essential to remember that the rates of climatic change and evolutionary change are normally unlike, or at least that this disparity has prevailed for a very long time past. The immense climatic changes which have occurred since the Pliocene period, for instance, have occupied an almost negligible portion of evolutionary time and are entirely out of proportion to the normal slow changes of evolution. That is to say, it is inconceivable that during this time evolutionary change and climatic change have continued *pari passu* but unrelately. Climatic change may have been the *cause* of evolutionary change, that is of the production of new forms, but these will, if they are indeed distinct forms, have by the Theory of Tolerance their own ranges of tolerance.

Actually the theory is of considerable interest in regard to the possible mechanism of species production. In the simple case described above there is a very great difference between the individuals in the van of movement and those in the rear. In the van the correlation between climate and area is never seriously upset; there is simply a gradually unfolding space into which dispersal can be effective. In the rear the conditions are quite different. Here the potential area is continually diminishing and the possibility of successful dispersal is, for many individuals, becoming increasingly small, so that the plants are constantly in incomplete harmony with their external conditions. They are, in short, in a state of environmental stress.

There is still no perfect understanding of the causes of the changes in genetic constitution which are the heralds of new morphological forms, but there is plenty of experimental evidence that such changes can be induced by external means and it at least seems possible that the conditions of stress outlined may do so.

This conception is a very important one. It was seen in Chapter 19 that climatic changes during the history of the Flowering Plants have been of two kinds, or rather of two degrees. There have been first of all the long-term gradual

secular changes which appear to be inseparable from the circumstances of cosmogony, and there have also been the rapid and catastrophic changes associated with periods of glaciation. These may well be reflected in two kinds of species formation, an equally gradual and inherent production of new forms in which time is the main factor, and the more rapid production of forms induced by the stress of catastrophic changes. This is in good accord with the view, frequently expressed, that the families of flowering plants are of two kinds, ancient and generalised, and modern and specialised, and may indeed be the explanation of this difference.

Although, as mentioned above, many species must have generally similar ranges of tolerance, any exact similarity between species in this respect is, if only on account of the number of factors involved, likely to be improbable, and even very slight differences may be of great significance. This being so, the influence of the tolerance relation will tend to be a selective influence, so that there is a sifting out of the species affected. As a result of this a climatic change need not be visualised as leading to equal movement among all of a large number of species, but as acting differentially, so as to increase the intermingling of floristic elements. Some species will be moved at a maximum rate while others will, to a more or less marked extent, lag behind, and hence there will tend to arise the blurring of floristic boundaries which is so characteristic a feature of plant distribution in many parts of the world.

The Theory of Tolerance also provides support for the views concerning the essentially limited real function of dispersal as described earlier. In terms of the theory, exceptionally wide dispersal is likely to be ineffective, because it will tend to deposit the disseminules in regions outside their potential areas, and they will therefore not establish themselves. Moreover dispersal, as a means of increasing geographical range, will probably be of appreciable value only in cases where the species has already occupied but part of its potential area. On the other hand, the minimum powers of dispersal required by the theory are no more than will suffice to enable the movement of species to keep pace with the movement of climatic zones, and there is every reason to suppose that even the smallest degree of dispersal is sufficient to do this.

It will, of course, be evident that in the attainment of the potential area barriers of various kinds must exercise a considerable influence. The symmetrical distribution of climatic values on both sides of the equator suggests that the potential area of many temperate species may in fact consist of two parts, one in the northern hemisphere and one in the southern, and that many of the plants confined to one or other have incomplete distributions. No doubt two causes contribute to this. First, there is the barrier presented by the tropical latitudes, a barrier across which the only obvious passage is by north-and-south mountain systems. Second, there is the constitution of the floras in the two temperate regions. The flora of each has undoubtedly developed more or less completely isolated from the other owing to the barrier just mentioned, and thus there tend to be corresponding plant forms occupying the corresponding niches in the vegetations of the two. As a result of this, competition to an intrusive species must almost certainly be exceptionally severe.

Two common observations bear directly on these points. Where a temperate genus is found in both hemispheres it will generally be noted that there are connecting species along one or other of the trans-tropical mountain systems; while southern temperate species commonly grow well in the north

in circumstances where the factor of competition is eliminated. The reverse is also true.

Although the paper enunciating the Theory of Tolerance and discussing its application to problems of plant geography appeared as recently as 1931, the conception on which the theory is based is implicit at least in many earlier writings. This has been pointed out by Wulff (269, 292), who, in the English summary of his memoir in Russian, gives several references, and especially one to the work of Engler (68). Certain more recent writers have expressed themselves even more definitely. Thoday (243), for example, writing of the genus *Passerina*, says, "the distribution of the species . . . indicates that each has a distinct physiological constitution and is specialized to a definite range of environmental factors." Salisbury, in a particularly important paper (206), makes frequent and direct allusion to the conception of tolerance, actually employing the phrase "climatic tolerance." He considers that a species has three zones of distribution: one where reproduction in full can take place; one where only vegetative propagation is possible; and one of cultivation where purely artificial reproduction is necessary. Thus he introduces the interesting subsidiary point that tolerance may not be the same in respect of all aspects of a plant's life and that, while certain conditions may suffice for ordinary vegetative growth, more particular values are necessary for reproduction. Since reproduction is the crucial stage of life, it is of course these latter values which will actually determine the distribution of the species. He mentions, too, the well-known fact that many garden plants do not flower because the special conditions necessary for this process are lacking, and also states that *Ranunculus Ficaria* reproduces by vegetative means near its northern limits of range. Even more interesting is his reference to *Stratiotes aloides*, of which he says that the male plants have a more northerly distribution than the females. Where they overlap there is seed production, but otherwise reproduction is vegetative.

Another noteworthy reference to tolerance is that of Hutchinson (135) in a paper with the significant title "Limiting factors in relation to specific tolerance of forest trees." He refers to Schimper's statement that "the differentiation of the earth's vegetation is thus controlled by three factors: heat, atmospheric precipitation including wind, and soil. Heat determines the flora, climatic humidity the vegetation; the soil as a rule merely picks out and blends the materials supplied by these two climatic factors, and on its own account adds a few details."

He goes on to discuss the distribution of many tree species in North America with special reference to their southern limits, and shows that many of these are coincident, while others intersect. In some precipitation seems clearly to be the determining factor, but others are also involved. He finally discusses various species particularly in relation to their tolerance, and gives several valuable diagrams illustrating the various points which emerge in the discussion.

The presentation of the Theory of Tolerance by the present writer (96) has been discussed at length by Wulff (269, 292), who deals with the history of the conception involved and emphasises a number of facts which in his opinion serve to support it. He also stresses the importance, not perhaps made sufficiently explicit in the original presentation of the theory, of the fact that climatic changes cause not only horizontal but also vertical plant movement, an effect that may lead to significant floristic mingling. It has also received lengthy consideration by Mason (161), who, working with special reference to the flora of California, has reviewed

the general principles therein set out and, in addition to making them more precise in their application, has increased their number to ten by including four based upon the acceptance of the Theory of Tolerance. In so far as these afford an amplification of the earlier exposition they may well be quoted in full here. They are, as the author points out, "organized under four headings. The first deals with the general subject of the environment in a dynamic sense, including the factors of the environment and the physical basis for their modification and control. The second group deals with the responses of the plant as governed by the Theory of Tolerance and the Principles of Limiting Factors. The third group is concerned with migration and establishment, and the fourth group deals with the perpetuation of vegetation, and the evolution of floras."

A. THE ENVIRONMENT OF THE PLANT.

1. Plant distribution is primarily controlled by the distribution of climatic factors, and in any given region the extremes of these factors may be more important than their means.
2. Plant distribution is secondarily controlled by the distribution of edaphic factors.
3. There has been great oscillation and variation in climate, especially in the higher latitudes, during the geological past.
4. At least some, and probably considerable, variation has occurred in the relative distribution and outline of the lands and seas in the geological past.

B. THE RESPONSES OF THE PLANT.

5. The functions governing the existence and successful reproduction of plant species are limited by definite ranges of intensity of particular climatic, edaphic and biotic factors. These ranges represent the tolerance of the function for the particular factor.
6. In the life history of the organism there are times when it is in some critical phase of its development which has a narrow tolerance range for a particular factor of the environment. The distribution of this intensity span of the factor during the time the plant is in this particular phase limits the area in which the function can operate, and hence governs the distribution of the species. The narrower the range of tolerance, the more critical the factor becomes.

C. THE MIGRATION OF FLORAS.

7. Great movements of floras have taken place in the past and are continuing to take place.
8. Migration is brought about by the transport of individual plants during their motile dispersal phases and the subsequent establishment of these migrules.

D. THE PERPETUATION AND EVOLUTION OF FLORAS.

9. The perpetuation of vegetation is dependent first upon the ability of the species to migrate, and secondly upon the ability of the species to vary and to transmit the favourable variations to their offspring.
10. The evolution of floras is dependent upon plant migration, the evolution of species, and the selective influences of climatic change acting upon the varying tolerances of the component species.

More recently the theory and, particularly, the principles of plant geography associated with it have been made the subject of an introductory chapter by Cain in his *Foundations of Plant Geography* (276) while the remainder of the book consists, to quote the author's own words, "in part, of an amplification of these principles with illustrative data and discussion, and such additional materials as compose the framework of plant geography . . . conceived as an explanatory science which attains its unity and justification by abstracting and synthesising from the contributions of more specialized sciences."

Cain begins with a further statement of principles, not only incorporating Mason's extended presentation but adding to them by raising to the status of principles three other generalisations familiar to plant geographers and ecologists. Two of these concern the environment, namely, (a) that biotic factors are of importance in controlling distribution, and (b) that the environment is holocoe-notic (that is to say that its factors do not act separately and independently but have mutual interactions and a concerted action upon organisms). The third, which concerns plant responses, is that different ontogenetic phases have different tolerances.

The Evidences of Tolerance

The Theory of Tolerance, it has been clearly shown, is intimately related to various evolutionary theories and shares with them the inevitable limitation that because of the immense time values involved no direct experimental proof is possible, and evidence must be circumstantial.

Actually the onus of proof is but a light one. The theory is built up on a generally accepted assumption of standing, and it may therefore be said that the reasons for the assumption may rank as evidence for the theory. These reasons are no more and no less than the observed facts of plant distribution as a whole and the impossibility of explaining them on any other basis, and the main thesis of the theory may therefore be considered to be upheld by the whole array of facts contained in the earlier chapters of this book.

As enunciated, however, the theory particularises the general assumption in various ways, and it is desirable to deal shortly with certain facts which support these more detailed opinions.

There is first the case of garden plants. These are habitually classified as hardy, half-hardy or tender, and there are no known instances of a plant departing from the behaviour which such terms imply. By half-hardy is meant roughly a limited tolerance to conditions of severe cold such as must be met by protection in the winter in such latitudes as those of Britain, or by germination in artificial heat of some kind. The point is that this half-hardiness is obviously a specific character, and a plant with such tolerance relations does not lose them on being transplanted from its native place to some other country. Moreover, this is a general character of the individuals of the species, and we do not find there is appreciable difference in tolerance between different plants. It may be that under cultivation some individuals may seem more resistant than others, but this can always be explained on the grounds that the conditions under which the species is growing are slightly different.

What is true of individuals may, however, not be true of the different strains of a species. Cultivated strains vary greatly in their tolerance, some being much more resistant than others to cold or other unfavourable conditions, and it is but

one aspect of the art of gardening to realise which are the appropriate strains to grow in varying circumstances. This, however, is exactly what might be expected according to the theory, because the strains are genetically distinct from one another and may be compared with incipient species, and their differences in tolerance are almost certainly reflected in their gene complement.

It may be urged that reference to cultivated plants is undesirable because of the artificial conditions in which they grow, but this really only increases their value as evidence, because the essential feature of cultivation is the removal of competition, a factor which always tends to obscure the relation of plants to external conditions in nature. In addition cultivated plants illustrate most vividly the way in which new forms can be induced by external means. It is true that cultivation may lead to an evolutionary change which in nature would have taken immeasurably longer, but this again is only in accordance with the theory.

What is true of the climatic portions of a plant's tolerance is also true of its relation to edaphic factors, and this also is commonly illustrated in horticulture. Every gardener knows that different plants need certain soil conditions and will tolerate no others, and that to grow plants otherwise is to court disaster. Here, again, closely related species may differ in requirement, but the individuals of the same species do not do so.

Both aspects of tolerance are combined in the general difficulty which is experienced in cultivating certain plants. Many most desirable garden plants either will not grow in gardens or glass-houses or only do so clearly under protest, and the explanation of this can hardly be other than that the resources of the cultivator are insufficient to provide the plant with the conditions which it needs. The greater the number and variety of plants to be cultivated, the greater the variety of facilities required for doing so. The scope of the ordinary outdoor gardener is comparatively limited compared with that of one who has a whole range of glass-houses, each reproducing some special condition, at his disposal.

One special aspect of this is of particular interest. Practical growers often believe that in the special circumstances of their work it pays to obtain the seed of a given species from a particular source and that this seed suits their special conditions and place of cultivation better than any other—that is to say that this seed produces plants more in harmony with the conditions available.

At first sight this may seem to cut across the thesis that all the individuals of a species have the same tolerance, but it actually affords one of the most interesting confirmations of it. As has been shown by experiment, the state of affairs described is generally due to the fact that the "species" comprises two or more strains, indistinguishable by visual characters but having definitely distinct ranges of tolerance, exactly the situation envisaged in paragraphs three and four of the theory (see p. 334).

Another important line of evidence is afforded by the subject of "acclimatisation." This, again, appears at first sight to be against the theory, but it can actually be explained quite simply in accordance with it. Species which do well in cultivation under conditions different from those in which they are found in a wild state are often supposed to have modified their external relations in conformity with their new surroundings. This is an unnecessary explanation. It has been shown that many species do not, for various reasons, occupy in nature the whole of their potential areas, and this means, in terms of the theory, that their tolerance to external conditions may be much wider than appears from a study of their natural

ranges. If this is so, then species may be grown artificially, especially in absence of competition, under conditions which do not exist in their natural habitats, because such conditions may be well within their tolerance although this fact is not apparent in nature. For instance, many South African plants can be cultivated out of doors in Britain. This does not necessarily imply that these species have altered their tolerances to accord with conditions in this country, but is explained on the assumption that such conditions are within the tolerances of the plants in question, although for reasons of topography or competition this is not apparent from their distributions in their native countries.

It is probable that many and perhaps all the supposed examples of acclimatisation are of this kind, and it is significant that many authorities have expressed the view that there is no such thing as real acclimatisation in the sense in which it is popularly meant. Hooker (126), for instance, says, "the fact now universally conceded by all intelligent horticulturists, that no plant has been acclimatized in England within the experience of man, is a very suggestive one. . . ."

Although considerations of hardiness and acclimatisation usually involve cultivated plants, there is an increasing amount of work on these problems in relation to wild plants. We have already mentioned one such (218), and another is the paper of Dexter and others (56) in which an interesting attempt to estimate frost resistance quantitatively is described. Of particular interest and importance, in that they bear very directly on the conceptions of the Theory of Tolerance, are also two papers by White, the second being largely a reprint of the first (259, 260).

White begins by referring to the common horticultural practice of using seeds collected from towards the northern limits of specific ranges to give the most cold-resistant seedlings, and instances the case of the black walnut (*Juglans nigra*). In this plant the individuals native to the southern States like Texas and Alabama are said to be incapable of living in such northern States as South Dakota and Minnesota. There are other cases of the same thing too, and there is distinct evidence favouring the belief that varieties, strains and geographical races, within species, vary considerably in their ability to resist cold (that is to say, in their tolerance to that external condition). White refers to de Candolle (39) in this connection, who finds no indication that perennial species have become adapted to greater cold and have thus extended their ranges northwards within the historical period, despite the fact that their seeds are continually being carried northwards. He quotes de Candolle's own words in which he says, "Periods of more than four or five thousand years . . . are needed apparently to produce a modification in a plant which will allow it to support a greater degree of cold."

White himself believes that the walnuts from the northern States may differ from those from the southern States by a gene or perhaps a series of genes that determines their ability to withstand different winter temperatures but in no other way expresses itself, at least so far as external characters are concerned. In other words, he supposes there may be two or more walnut genotypes indistinguishable at sight but restricted geographically by the nature of their tolerance to cold, and thus visualises exactly one of the conditions postulated in the enunciation of the Theory of Tolerance. He thinks it probable, moreover, that many tropical and warm-temperate species give rise, by mutation, to individuals much more cold-resisting and that these remain for the most part unrecognised because they occur and grow under conditions where the character in question

could not be expressed. If this is so, then the Pleistocene glaciation would have a sifting effect, some genera being able to continue living in what would appear to be more rigorous conditions, while others would be destroyed there, only later reimmigrating from the south as they produced more hardy genotypes by mutation (156, 157).

He mentions a number of plants which, having a wide north-south range, are known to have hardy and less hardy forms, and also points out that if a species is restricted in its range by conditions other than temperature it may in fact be much more resistant to cold than its natural range indicates. Also, since some wide-ranging species are apparently without different forms, species may clearly be of two types as regards their resistance to temperature. In one type all the individuals can exist over a wide range of temperature, but in the other the species is composed of numerous groups, each with its particular temperature range, although these groups are indistinguishable morphologically.

Finally he refers to a number of species which occur over a wide range of temperature, such as *Tillandsia usneoides*, *Asimina triloba* and *Nymphaea odorata*, and to species which are tropical in natural range but which on cultivation prove to be unexpectedly hardy. Among these latter he cites *Leitneria floridana*, *Gleditsia aquatica*, *Lavandula Spica*, *Yucca filamentosa*, *Maclura pomifera*, *Magnolia grandiflora*, *Hamamelis vernalis* and *Nymphaea mexicana*.

What is generally looked upon as incomplete acclimatisation is also explicable in terms of the theory. There are exotic species which when cultivated in this country maintain themselves successfully until a particularly severe climatic condition destroys them. One explanation at least is that normal conditions are within their tolerance ranges but that exceptional conditions are outside it, with disastrous results to the plants.

The conception of ecesis, or adaptation to environment, also infers the application of the Theory of Tolerance. Many species have a peculiar and particular morphological structure which, so far as can be seen, enables them to inhabit certain equally definite types of habitat or to live under equally definite conditions. It is generally believed that these structures have the effect of thus restricting the species possessing them. This is tantamount to saying that these species can exist only in these special habitats or conditions, at least while their peculiar morphology persists, and this in turn is equivalent, in fact at least, to an acceptance of the main thesis.

Next, the early researches of Klebs on phasic development in plants, and their recent great elaboration by Lysenko and other Russian workers (273) in connection with the vernalisation of seeds, have a very direct bearing upon the conception of tolerance.

Lysenko's work and views have now been presented in the form of a theory of which the most important and apposite portions are as follows. Lysenko believes that the growth of a plant is not a single and simple process of increase in quantity but is in fact made up also of a series of stages at each of which changes of a qualitative nature occur. These two he distinguishes as "growth" and "development." The two may go on dependently or independently and plants may show rapid growth but slow development, slow growth but rapid development, or rapid growth and rapid development. The culmination of the life of the plant is the production of ripe fruit, and this particularly is believed to be achieved only by the fulfilment of each of a number of developmental stages. Moreover, these stages always proceed in one order and no stage can be initiated until the proper

preceding one has been completed. Finally, the most important postulate from our point of view is that different stages of development of the same plant require for their completion different external conditions.

For any detailed account of vernalisation the reader must refer to other works, of which perhaps the most convenient are the *Bulletins of the Imperial Bureaux of Plant Genetics* (166, 261, 272, 273), but a very brief account is of sufficiently direct relation to geographical problems to warrant inclusion here.

The time that it takes for an individual plant to pass from the condition of a dry seed to that of producing ripe fruit—that is to say, the time which must elapse between sowing and reaping—obviously depends (on the old view) upon the rapidity of growth, but according to the theories just described it depends more accurately upon the time occupied by each of the developmental stages through which the plant has to pass during its life. In the ordinary way much of the time is occupied by the period between sowing and the emergence of the seedling above ground. According to the modern view this period is in fact one of the developmental stages and during it the seed must be provided with certain definite conditions, and until these are fulfilled it will not proceed to the next stages of development. In theory, then, if the seed's requirements at this stage can be discovered, it should be possible to provide the seed with them before it is sown. In other words, it should be possible to make the seed pass through this initial stage in development before it is put in the ground, so that when it is so planted it will almost immediately germinate. This has actually been done with a number of crop plants, especially some of the cereals, and is the process known as vernalisation. Vernalised seeds therefore take a shorter time to come to fruition after they are sown, and it need hardly be said that this is a consideration of the utmost importance. Especially is it so in countries where the latitude gives so short a growing season that many crops cannot reach maturity in the time available. If the growth period can be shortened, then many crops may be grown that would otherwise be impossible.

This state of affairs prevails over much of Russia, and this is the reason why vernalisation and related problems have received so much attention from Russian scientists. It should perhaps be emphasised that vernalisation does not in any way alter the developmental necessities or stages of the plant. Its value lies in the fact that it permits the first stage of development to be carried out when and where required and before external conditions allow of ordinary sowing in the field.

The importance of these theories and of vernalisation to the Theory of Tolerance is the very important supporting evidence they provide that the individual plant and also each species as a whole require certain perfectly definite external conditions for their development, and that without those particular conditions they cannot mature. There are, of course, plenty of other indications that this is so, and the special importance of Lysenko's work is in the demonstration it affords that the life of the plant is divided into a number of stages each of which not only requires exact external conditions but more often than not quite different external conditions. This means that different external conditions will be crucial to the plant at different stages in its history, and its tolerance must be sometimes even more detailed and exact than appears at first sight. For instance, according to the researches described, the first stage in development is intimately connected with temperature and moisture values, while the second involves more deeply than anything else the factor of light.

Finally, there is the belief widely held by palaeobotanists, and the basis for much of their hypothesis and determinations, that the occurrence of fossils similar to or identical with living plants indicates that the conditions under which they existed were similar to or identical with the conditions under which their modern counterparts exist to-day. This opinion has already been mentioned, not only in Chapter 14 but also as one line of evidence for climatic change in the past. It is true that there is little direct evidence for the view, but it is nevertheless generally accepted in broad outline. It is important here because tacitly, if not admittedly, it is based upon the primary postulate of the theory, namely that the relation of a species to external conditions is a character of that species and that it may persist unaltered as long as morphological features persist. Actually it will be realised that this belief involves an even more rigid outlook than is required by the theory, in that it does not allow due latitude for the *possibility* of tolerance change without morphological change during time of evolutionary magnitude.

Summary

From the discussion of the Theory of Tolerance in the foregoing pages the following three major conclusions emerge.

First, the main thesis, that any species shows a definite range of tolerance to external conditions at any given time is scarcely to be denied, because the whole picture of plant distribution is so intimately related to the distribution of external factors that no other view can reasonably be maintained.

Second, supporting evidences of this, if they are needed, are furnished by the behaviour of plants in cultivation ; by the non-occurrence of "acclimatisation" ; by the whole conception of "adaptation to environment" ; and by such matters as phasic development and vernalisation.

Third, certain more detailed aspects of the application of the theory are more debatable. In particular the value of the theory as an *explanation* of phytogeographical facts stands or falls by the subsidiary hypothesis which postulates that environmental change has, at least during the more recent past, been more rapid than change in tolerance or morphology, or, in other words, by the view that progressive adaptation to external change has not had time to occur *in situ*.

Clearly the problem here involves the past as well as the present, and it is to palaeobotany that we must turn in search of evidence. This is not far to seek. The history of the British flora since the latter part of the Tertiary epoch amounts, by itself, to almost conclusive evidence in support of this thesis. It shows clearly that since Pliocene times species have altered but little morphologically, yet in the same period there have been drastic changes in climate and environment. It is surely beyond the bounds of reasonable probability to suggest that tolerance has varied coincidentally with and proportionately to these changes, but has been virtually entirely unaccompanied by morphological change. Were this indeed the case it would inevitably be betrayed, either rarely or more commonly, in the habits and habitats of living plants. In fact all these, as has been demonstrated in the last few pages, point to the reverse, and this being so, this second and more particular postulate of the Theory of Tolerance may also be claimed to be the truth.

But it is this particular part of the general theory which converts the whole,

at least as regards plant geography, from a mere conception to a means of elucidation, because, if it is accepted, it is possible to construct in the way indicated in the earlier pages of this chapter a general explanation of the facts of plant geography and, as will be done in the next and final chapter of this book, to weave into one single pattern the many diverse and separate threads of the subject.

CHAPTER 22

CONCLUSIONS

It is the task of this final chapter to attempt a synthesis of all that has gone before and to present to the reader a brief but comprehensive summary of the processes and events which have led to that state of plant distribution observable to-day. On first considerations such a task may, with reason, seem almost impossible, so great and multifarious is the mass of fact and theory to be taken into account. But by carefully sorting and sifting the material a gradual outline emerges, and this outline becomes clearer with every increment to our knowledge.

The form which that outline takes has been made sufficiently apparent by the discussions which form so large a part of Chapters 15 to 21, and from these, reinforced by the innumerable facts cited in earlier chapters, it is possible to paint a picture which may claim at least some degree of completeness.

First and foremost we must visualise the constant production of new forms (the systematist's species) by the processes of evolution. This is as it were the primary determinant of the picture; it is the medium in which it is painted. This must be so because the very appearance and development of the great group of the Flowering Plants is an expression of it. It is the fundamental cause of the geographical facts which we observe.

The picture must therefore have as its background the historical development of these plants, and this, in so far as it has been revealed, can be described fairly shortly.

Some time in the middle or later parts of the Mesozoic epoch there arose, presumably from some already existent type of seed-plant, a group of plants characterised by possessing special closed structures known as carpels, and having other associated features. Thus there came into being the group of plants—the Angiosperms or Flowering Plants—destined in a very short time to become the dominant vegetation throughout the land surfaces of the globe.

Of this actual origin very little is known. There are indications here and there in the rocks of what may be regarded, with varying certainty, as forerunners or ancestral types, but the Flowering Plants proper appear with bewildering suddenness in the deposits of the later Cretaceous. In the horizons below this they are few; in this and succeeding horizons they predominate to a greater or lesser extent and indeed almost at once attain that position in the general vegetation that they hold to-day. The reason for this sudden appearance is not clear, nor need it detain us here. It is enough to know that the Flowering Plants have been the dominant world group since the end of the Mesozoic era.

For the reasons which have been explained in Chapter 14, caution must be exercised in making deductions from the fossil record, but there are strong indications on this and other evidence that the earlier Flowering Plants were mostly woody plants of a mesophytic nature, that is to say living in generalised and medium climatic conditions. The great herbaceous families of to-day, associated as they so often are with extreme climatic conditions, such as lack of water and extreme cold, are practically unrepresented in the earlier parts of the fossil

record of the Angiosperms, and on this ground at least may be considered as a later development.

This is in accordance, moreover, with what is known of the climates of the past. There are cogent reasons for believing and it is generally accepted to-day that the later Cretaceous and all but the latter part of the Tertiary period were a time of relatively constant or but slightly fluctuating climates, characterised by genial, moist conditions varying little with the passage of time and associated with a minimum of relief on the world's surface.

The Angiosperms, then, may be pictured as originating and slowly diversifying for millions of years, comparatively little affected by changes in their external circumstances, and it is believed that during this period the main outline of the group as it is seen to-day was determined. It was, as has so frequently been said, an age of generalisation—an age of natural evolution by the inherent processes of change with time.

During this period there is little doubt that the distribution of the flowering plants was also far more generalised than it is to-day. Temperature and other climatic gradients were everywhere more gradual, and there is reason to think that what are now called temperate conditions, with their accompanying vegetation, reached almost if not quite to the poles.

In terms which have been frequently used above, potential areas were probably much larger, much more extensive, and their attainment was much less impeded by barriers. Mountains were lower and their climatic effects less pronounced. In addition there is a general belief that the land surfaces of the globe were less scattered. As to this last belief, it is only the explanation which is contentious. An older school believes in the former existence of connecting land surfaces which have now disappeared. The more modern belief is that the continents have drifted away from one another. Whichever is correct—and there is an ever-increasing movement towards the latter view—it is generally accepted that geographical isolation, which is the direct result of the separation of land-masses, has increased to what may be regarded as a maximum to-day.

With this increasing isolation came, inevitably, local specialisation by the effects of segregated and isolated evolution, and this was probably the first kind of specialisation superposed on the earlier generalised distribution of the Flowering Plants.

All this time the distribution of plants was being attained almost entirely by spread in all directions by means of dispersal, this dispersal being directed and controlled by external factors only to a minimum extent. It may, indeed, be described as essentially a period in which this newly evolved group of plants multiplied, and in doing so established something like a geographical equilibrium with the fairly constant external conditions. It was a period of steady and widespread colonisation of the land surfaces of the globe by a new and superior type of vegetation.

It is no exaggeration to say that towards the end of the Tertiary epoch the picture changed in almost every respect. At that time causes of which little is known brought on one of the periodical catastrophic periods which there seems little doubt have been an intermittent feature of all past time.

The catastrophe consisted of a drastic and, in a geological sense, sudden alteration in the temperature relations of the world's surface, a change which brought in its train all kinds of minor and secondary variations. It culminated in what is called a glacial period during which, certainly for the first time in

the history of the Angiosperms, glacial conditions developed at sea level near the poles.

It is possible that equatorial temperature values were but little affected, but, whether this is so or not, it is certain that the main result of the change was to telescope up the latitudinal zonation of climate. That is to say the slight gradient from the equator to the poles was replaced by a steep gradient culminating at higher latitudes in what are now called arctic and antarctic conditions. From the point of view of the vegetation this meant a marked diminution in the areas available for the different sorts of plants and the diminution nearly everywhere of the average size of potential areas.

It is unlikely that the effects were felt everywhere equally. In some parts of the northern hemisphere, for instance, the effects of the polar ice-cap were felt far less than elsewhere, but it is safe to say that nowhere was its influence entirely negligible.

This great climatic change was heralded or anticipated by a period of intense mountain building such as has also been an intermittent feature in world history. This process is generally associated more particularly with the Miocene period, and from it date practically all the great mountain systems of the world to-day. Their effect on the climate also was, quite apart from the subsequent glaciation, immense.

Not only were appreciable areas of the earth's crust raised into colder layers of the atmosphere but, even more important, the newly elevated mountain ranges intercepted the moisture-laden winds from the oceans and condemned many parts of the interior of the continents to aridity.

These changes in turn brought alterations in all sorts of other climatic aspects, such as those of pressure and wind, and every kind of external condition for plant life suffered some modification.

It may well have been in direct association with these orographic and climatic changes that changes in the distribution of land and sea were especially notable, and there is even some reason to suggest that continental drift and displacement may have been an essential feature of this period, and even perhaps was initiated then rather than earlier.

The effect of all this on the Flowering Plants was profound. Everywhere their long-familiar world and surroundings were changed, and survival in the face of such disasters became the main theme and problem of their life. Those, for instance, living at the higher latitudes were faced, almost certainly for the first time, with the problem of frost, a danger which it can scarcely be doubted they were unequipped to meet. Moreover, their potential areas were everywhere being moved under the influence of climatic change. Rarely could this movement be unaccompanied by change in area, and with the general shrinking of the more genial parts of the world there was an almost inevitable general tendency to shrinking of their potential areas. More than this, some of them no doubt were completely eliminated.

Everywhere conditions of stress as between plant and environment became inevitable. These were least, no doubt, in the equatorial regions, and it is noteworthy that it is the vegetation of this zone which to-day is considered on quite other grounds to be the most *primaeval*, but they must have been felt to some degree almost everywhere.

There can be little doubt that this had a profound effect not only on the results of evolution in the Flowering Plants but also, it may be, on the processes of evolu-

tion themselves. No longer can evolutionary change be pictured as something inherent and perhaps unrelated to external conditions. No doubt this type of evolution continued, as indeed it must, but the changes which it produced were henceforth to be judged by the stern test of practical success. Such changes as contributed appreciably to increasing the correlation between plant and environment were effective; those which had no such value, or which, owing to external conditions, may have had an opposite import, were ineffective. There thus arose quite a different conception of evolution: the conception of something which was capable in certain circumstances of meeting the dangers to which the plants involved were exposed.

Similarly the factors of distribution took on new rôles and new values. The potentiality for dispersal became, with the increasing heterogeneity of external conditions, of less significance. Range of tolerance, on the other hand, must have increased in importance. Distribution of land and sea became a matter of great moment, determining as it did the directions of possible retreat from danger. Changes of climate not only enforced migration but also partly at least determined its direction.

It is perhaps permissible to summarise what has been said by asserting that while in the pre-glacial portion of their history the Flowering Plants were the masters of their environment, in the sense that they were probably, to some extent at least, in equilibrium with it, their post-glacial history saw the development of the reverse state of affairs. No one general feature of plant development and distribution since the Pliocene is so prominent as the marked lack of equilibrium between vegetation and its environment. This must not be taken to mean that many plants are not peculiarly and beautifully adapted to their surroundings. This fact is rather to be emphasised as indicating how far from general adaptation of this kind is.

Returning to the difference in evolution mentioned above, there is ample evidence that mutation, which is often the physical basis of new forms, can be induced at unusual rates by the application of certain external factors, and especially by changes in external factors. It can scarcely be denied that the changes consequent upon the Pleistocene glaciation constituted such influences and that they may thus have greatly accelerated the production of new forms by this method. The species constitution of some genera, especially, be it noted, those living in what were once glaciated regions, can indeed hardly be explained on any other basis.

But no matter what the aspect, the constitution of groups as well as their distribution everywhere reflects the disastrous result of the ice ages. The extraordinary development of many herbaceous types, and especially of those with well-marked methods of perennation, seems clearly to be correlated with a distribution of climatic conditions such as would put a premium on the possession of these features. In particular, perhaps we may mention many semi-desert families and genera, as well as many constituents of the more northerly temperate or subarctic zones. Again, it is probable, as has been shown, that the arctic flora and to a certain extent the alpine flora as known to-day are to be regarded as a consequence of the glacial ages. Yet again, there is clear evidence that this time brought in its train extensive annihilation of plants in many parts of the world. That, for instance, is the generally accepted explanation of the poverty of the European flora (as distinct from the purely Mediterranean) compared with that of eastern North America and eastern Asia, and there are many other examples.

No longer then is the development of the Flowering Plants something that is proceeding with a slow, stately, and inevitable progress scarcely modified by the more detailed aspects of environment. On the contrary, to-day this development must be visualised as something everywhere controlled by factors beyond the response of the plants themselves. As with evolution, so with distribution. The distribution of plants to-day gives every evidence that it is in a state of almost complete flux. The movement of species and of floras over the world is everywhere being forced upon them by the exigencies of environmental change, and everywhere the plants can survive only by keeping pace with this movement, or by giving place to new forms less critically affected by these conditions. As has been said, all these influences appear, as might be expected, to be expressed least in the equatorial regions and, conversely, are most marked in the higher latitudes, and this is in accord not only with the story which has been outlined here but also with the assumptions of plant relationship and phylogeny based upon and derived from other sources.

In a word, the distribution of plants to-day unquestionably suggests that the Flowering Plants are recovering from a catastrophe, and that they are actively in process of reconstituting that generalised balance or equilibrium between vegetation and environment which has been pictured above as the outstanding feature of pre-glacial plant geography. So far the period of recovery has been very short and one can only be amazed at the progress which the plants have made in the course of it. Whether it will continue at its present rate to its culmination without setbacks or whether fresh disasters are still to come cannot and will not be revealed, but that eventually, though perhaps only after the passage of enormous time, such result will be achieved can scarcely be doubted. Whether the Angiosperms will still be recognisable or whether they will, before then, have given place in the process to some still more highly developed group is a question which admits of no answer now.

APPENDIX A

Statistics of the World's Land Surfaces

If the latitudinal and altitudinal zonations described in the early pages of Chapter 2 are modified, for statistical purposes, into simpler and rounder figures, it is possible to obtain from a paper by Murray (175) a useful and reasonably accurate mathematical impression of the proportionate distribution of the more important climatic types of vegetation at different latitudes.

Let it be assumed then for this purpose that latitudinal zonation is expressed sufficiently accurately as follows :

0°-20°	Tropical ;
20°-40°	Subtropical and warm temperate ;
40°-60°	Temperate ;
60°-80°	Arctic and antarctic ;

and that altitudinal zonations may be set out in the following scheme :

In the tropical zone	0- 3,000 ft. bears tropical vegetation.
	3,000- 6,000 ft. „ subtropical vegetation.
	6,000-12,000 ft. „ temperate vegetation.
	12,000-18,000 ft. „ arctic-alpine vegetation.
In the subtropical zones	0- 3,000 ft. bears subtropical vegetation.
	3,000- 6,000 ft. „ temperate vegetation.
	6,000-12,000 ft. „ arctic-alpine vegetation.
In the temperate zones	0- 3,000 ft. bears temperate vegetation.
	3,000- 6,000 ft. „ arctic-alpine vegetation.
In the arctic zones	0- 3,000 ft. bears arctic-alpine vegetation.

On the basis of these classifications the relevant figures from Murray can be arranged in a series of tables.

TABLE 1.

Total Land Surfaces of the *Latitudinal* Zones, in Thousands of Square Miles.

80°-90° N.	112 (no flowering plants)
70°-80° N.	1,379
60°-70° N.	4,767
50°-60° N.	5,300
40°-50° N.	6,225
30°-40° N.	6,436
20°-30° N.	5,773
10°-20° N.	4,278
0°-10° N.	3,832
0°-10° S.	3,973
10°-20° S.	3,630
20°-30° S.	3,550
30°-40° S.	1,659
40°-50° S.	408
50°-60° S.	87
Antarctic continent	3,565 (no flowering plants)

TABLE 2.

Total Land Surfaces of the Main *Vegetation Zones*, in Thousands of Square Miles.

North arctic-alpine	6,146
„ temperate	11,525
„ subtropical	12,210
„ tropical	8,110
South tropical	7,605
„ subtropical	5,208
„ temperate	495
„ antarctic-alpine	—

Or, combining the equivalent zones in each hemisphere :

Arctic- and antarctic-alpine vegetation zones	.	6,146
Temperate zones	.	12,020
Subtropical zones	.	17,418
Tropical zones	.	15,715

that is to say, in rough proportion :

arctic-alpine 1 ; temperate 2 ; subtropical 3 ; tropical 2·5.

The next table shows the figures further analysed and segregated according to altitude as well as latitude :

TABLE 3.

Areas open to the several *Vegetation Types* at different *Latitudes*.

	No Vegetation	Arctic- alpine	Temperate	Subtropical	Tropical	Total
80°-90° N.	112	—	—	—	—	112
60°-80° N.	729	5,417	—	—	—	6,146
40°-60° N.	895	2,137	8,493	—	—	11,525
20°-40° N.	921	1,487	2,318	7,485	—	12,211
0°-20° N.	1	24	326	1,188	6,571	8,110
0°-20° S.	17	193	261	1,583	5,551	7,605
20°-40° S.	110	180	652	4,266	—	5,208
40°-60° S.	28	63	404	—	—	495
60°-80° S.	—	—	—	—	—	—
80°-90° S.	—	—	—	—	—	—
Totals	2,813	9,501	12,454	14,522	12,122	51,412
Northern hemisphere	2,658	9,065	11,137	8,673	6,571	38,104
Southern hemisphere	155	436	1,317	5,849	5,551	13,308

Finally it is worth while to show the proportion of the land in each zone which, *on account of elevation*, is not occupied by the type of vegetation characteristic of the zone at sea level. The figures are :

North temperate	about one-fourth
North subtropical	„ three-eighths
North tropical	„ one-fifth
South tropical	„ one-quarter
South subtropical	„ two-elevenths
South temperate	„ two-elevenths

The chief points emerging from the foregoing tables are :

1. Excluding the arctic and antarctic, there is two and a half times as much total land in the north as there is in the south.

2. There is virtually no available land south of 60° S.
3. Land sufficiently high to bear arctic-alpine vegetation occurs in all zones, but by far the smallest proportion is in the north tropics.
4. The total area of temperate vegetation in the northern hemisphere is between eight and nine times as great as in the southern.
5. The total area of arctic-alpine vegetation in the northern hemisphere is more than twenty times as great as in the southern.

APPENDIX B

Discontinuous Genera

THE following is a second and revised edition of the list of widely discontinuous genera published in the *New Phytologist* (92). As there, authorities for the names are given; genera which are to be considered *in sensu stricto* are indicated by asterisks; and certain pairs of genera are combined. In addition the comparable figures in each of the two editions are given at the end of each major and minor category.

The main differences between the two lists are: the exclusion from the second, for various reasons, of the following genera or pairs of genera which appeared in the first, i.e. *Adenochlaena*, *Aerva*, *Alisma*, *Blepharis*, *Boottia*, *Brunnichia*, *Byblis* and *Roridula*, *Courtoisia*, *Dioclea*, *Hymenocallis*, *Jasminum*, *Marica*, *Mohlana*, *Rhipsalis*, *Rochelia* and *Maccoya*, and *Stillingia*; and the inclusion in this second list of about 65 genera or pairs which do not appear in the first. There is thus a net increase of about 50 genera. The chief purpose of the names and, particularly, the authorities given being to define the groups of species intended as unmistakably as possible for those readers who may not be expert taxonomists, I have, in general, used those which seem most likely to achieve this aim, even if they are not those which, according to the strict letter of the Rules of Nomenclature, should be cited.

A. Genera found entirely or predominantly in the North Temperate Zone.

a. Discontinuous over the whole North Temperate Zone.

Aesculus L. and *Hippocastanum* Rupp., *Apocynum* L., *Bifora* Hoffm., *Carpinus* L., *Cercis* L., *Fagus* L.*, *Gleditsia* Clayton, *Harrimanella* Cov., *Hypopitys* Dill., *Liquidambar* L., *Nartheceum* Moehr., *Ostrya* Scop., *Paeonia* L., *Philadelphus* L., *Pistacia* L., *Staphylea* L., *Tilia* L. 17 (16)

b. Europe and/or W. Asia and E. Asia.

Bosea L. and *Rodetia* Moq., *Epimedium* L., *Forsythia* Vahl, *Leontopodium* R. Br., *Meconopsis* Vig.*, *Parrotia* C. A. Mey. and *Fothergilla* Murr. p.p., *Pterocarya* Kunth, *Theligonum* L., *Wulfenia* Jacq., *Zelkova* Spacht 10 (6)

c. N. America, Europe and W. Asia.

Ammophila Host, *Arbutus* L., *Cakile* Mill., *Cinna* L., *Comandra* Nutt., *Corema* D. Don, *Datisca* L., *Douglasia* Lindl., *Eryngium* L., *Eurotia* Adans., *Heberdenia* Banks, *Helianthemum* Tourn., *Hottonia* L., *Loeflingia* L., *Lupinus* L., *Peganum* L., *Platanus* L., *Spartina* Schreb.*, *Specularia* Heist. 19 (17)

d. N. America (especially or entirely in the West) and in Central and/or E. Asia.

Boschniakia C. A. Mey., *Boykinia* Nutt., *Chamaesaracha* A. Gr., *Clintonia* Raf., *Dicentra* Bernh., *Echinopanax* Decne. et Planch., *Enemion* Raf., *Glehnia* Schmidt, *Mahonia* Nutt., *Mitella* L., *Monotropa* L.*, *Nephrophyllidium* Gilg, *Phyllospadix* Hook., *Stenanthella* Rydb., *Thermopsis* R. Br., *Tiarella* L., *Trillium* L. 17 (13)

e. Eastern N. America and both continental and insular E. Asia.

Amsonia Walt., *Apios* Moench, *Buckleya* Torr., *Calycanthus* L. and *Chimonanthus* Lindl., *Caulophyllum* Michx., *Cladrastis* Raf., *Cryptotaenia* DC., *Diervilla* Mill. and *Weigela* Thunb., *Hamamelis* L., *Houttuynia* Thunb. and *Anemopsis* Hk. et Arn., *Kraunhia* Raf. and *Wisteria* Nutt., *Menispermum* L., *Pachysandra* Michx., *Panax* L., *Penthorum* L., *Phryma* L., *Podophyllum* L., *Pogonia* Juss., *Saururus* L., *Shortia* Torr. et Gr., *Stewartia* L., *Symplocarpus* Salisb., *Tipularia* Nutt., *Triosteum* L., *Zanthoxylum* L.* 25 (24)

f. Eastern N. America and continental E. Asia only.

Aletris L., *Campsis* Lour., *Chionanthus* L., *Decumaria* L., *Gymnocladus* Lam., *Halesia* L., *Jeffersonia* Barton, *Liriodendron* L., *Pyrularia* Michx., *Stylophorum* Nutt. 10 (9)

g. Eastern N. America and Japan only.

Achlys DC., *Arethusa* L., *Chiogenes* Salisb., *Croomia* Torr., *Diarrhena* Beauv., *Diphyllia* Michx., *Epigaea* L., *Hydrastis* Ellis and *Glaucidium* Sieb. et Zucc., *Mitchella* L., *Trautvetteria* Fisch. et Mey., *Triantha* Bak. 11 (10)

h. Eastern N. America and E. Asia, with extensions into the tropics of one or both hemispheres.

Abelia R. Br., *Aralia* L., *Astilbe* Buch.-Ham., *Berchemia* Neck., *Catalpa* Scop., *Disporum* Salisb., *Gelsemium* Juss., *Gordonia* Ellis, *Halenia* Borkh., *Hydrangea* L., *Illicium* L., *Itea* L., *Ligustrum* L., *Magnolia* L., *Nelumbo* Adans., *Nyssa* L., *Photinia* Lindl.*, *Schisandra* Michx. 18 (20)

B. Genera found entirely or predominantly in the tropical regions, but excluding pantropical genera.

a. America, Africa and/or Madagascar, etc.

1. America, Africa and Madagascar, etc.

Ascolepis Steud., *Astephanus* R. Br., *Bertiera* Aubl., *Caperonia* St. Hil., *Carpodiptera* Griseb., *Cassipourea* Aubl. and *Weihea* Spreng., *Eichhornia* Kunth, *Elaeis* Jacq., *Eulophidium* Pfitz., *Hirtella* L., *Landolphia* Beauv., *Loudetia* Steud., *Melinis* Beauv., *Mostuea* Didr. and *Leptocladus* Oliv., *Paullinia* L., *Pentodon* Hochst., *Piriqueta* Aubl., *Raphia* Beauv., *Sabicea* Aubl., *Savia* Willd., *Symphonia* L., *Trachypogon* Nees, *Trichilia* L., *Tristachya* Nees, *Vellozia* Vand. and *Barbacenia* Vand. 25 (24)

2. America and continental Africa only.

Amanoa Aubl., *Andira* Lam., *Antheophora* Schreb., *Aptandra* Miers, *Asclepias* L., *Bartsia* L.*, *Bouchea* Cham.*, *Brachypterys* A. Juss. (?), *Buforrestia* C. B. Cl., *Cacocua* Aubl., *Chlorophora* Gaudich., *Chrysobalanus* L., *Conocarpus* L., *Copaifera* L., *Corrigiola* L., *Drepanocarpus* G. F. Mey., *Eriochrysis* Beauv., *Euclasta* Franch., *Gentlesea* St. Hil., *Guarea* Allem., *Heisteria* Jacq., *Heteranthera* R. et P., *Heteropteris* H., B. et K., *Hoffmanseggia* Cav., *Hydranthellium* H., B. et K., *Hypogynium* Nees, *Laguncularia* Gaertn. f., *Lindackeria* C. Presl, *Macrolobium* Schreb., *Malouetia* A. DC., *Maprounea* Aubl., *Mayaca* Aubl., *Melasma* Berg.*, *Microtea* Sw., *Neurotheca* Salisb., *Ochthocosmus* Benth. and *Phyllocosmus* Klotzsch, *Olyra* L., *Parkinsonia* L., *Pentaclethra* Benth., *Pitcairnia* L'Hérit. (?), *Prevostea* Choisy, *Priva* Adans., *Ptychopetalum* Benth., *Quassia* L., *Renealmia* L.f., *Saccoglottis* Mart., *Schaueria* Nees, *Schultesia* Mart., *Sclerocarpus* Jacq., *Sparganophorus* Crantz, *Sphaeralcea* St. Hil., *Symmeria* Benth., *Syngonanthus* Ruhl., *Talinum* Adans., *Tapura* Aubl., *Thalia* L., *Thamnosma* Torr. et Frém., *Trianosperma* Mart., *Tristicha* Thou., *Trymatococcus* Poepp. et Engl., *Vismia* Vand., *Voyria* Aubl. and *Leiphatmos* Ch. et Sch. 62 (63)

3. America and Madagascar only.

Paepalanthus Mart., *Pedilanthus* Neck., *Ravenala* Adans. and *Phenakospermum* Endl., *Rheedia* L. 4 (4)

b. Africa, Asia and/or Madagascar, etc.

1. Africa and Asia (often extending into Australasia and the Pacific Islands).

Adenanthera L., *Adina* Salisb., *Adinandra* Jack, *Aegle* Corr. and *Afraegle* Engl., *Alstonia* R. Br., *Ancistrocladus* Wall., *Anogeissus* Wall., *Antiaris* Lesch., *Aphania* Bl., *Argostemma* Wall., *Artanema* D. Don, *Baissea* A. DC., *Bowringia* Champ., *Brachylophon* Oliv., *Brackenridgea* A. Gr., *Brucea* J. F. Mill., *Bryonopsis* Arn., *Cajanus* DC., *Calamus* L., *Capillipedium* Stapf, *Centotheca* Desv., *Clausena* Burm. f., *Cleistachne* Benth., *Coccinia* Wight et Arn., *Combretodendron* A. Chev., *Ctenolophon* Oliv., *Cyanotis* D. Don, *Cyrtococcum* Stapf, *Dalhousiea* R. Grah., *Dichanthium* Willemet, *Dovyalis* E. Mey., *Droogmansia* De Wild., *Elatostema* Forst., *Elsholtzia* Willd., *Elytrophorus* Beauv., *Englerastrum* Briq. *, *Epithema* Bl., *Erythrophleum* Afzel., *Fingerhuthia* Nees, *Firmiana* Marsigli, *Flacourtia* L'Hérit., *Flemingia* Roxb., *Fluggea* Willd., *Geissaspis* Wight et Arn., *Halopegia* K. Sch., *Harrisonia* R. Br., *Heritiera* Ait., *Holarrhena* R. Br., *Hunteria* Roxb., *Hymenocardia* Wall., *Illigera* Bl., *Kaempferia* L., *Kedrostis* Medik., *Lasianthus* Jack, *Lecanthus* Wedd., *Lepistemon* Bl., *Leptonychia* Turcz., *Limonia* L. and *Citropsis* Swingle et Kellern., *Mallotus* Lour., *Manisuris* L., *Mansonia* J. R. Drum., *Microdesmis* Hk. f., *Milletia* Wight et Arn., *Mitragyna* Korth., *Monochoria* C. Presl., *Musa* L., *Naregamia* Wight et Arn., *Neuropolitis* Medik., *Opilia* Roxb., *Oropetium* Trin., *Orthanthera* Wight, *Ottochloa* Dandy, *Oxytenanthera* Munro, *Parochetus* Buch.-Ham., *Perotis* Ait., *Petalidium* Nees, *Platostoma* Benth. et Hk., *Pterolobium* R. Br., *Pterygota* Schott et Endl., *Pygeum* Gaertn., *Pyrenacantha* Wight, *Quisqualis* L., *Ranalisma* Stapf, *Remusatia* Schott, *Rothia* Pers., *Roureopsis* Planch., *Sansevieria* Thunb., *Santaloides* Schellenb., *Sarcocephalus* Afzel., *Sauromatum* Schott, *Schoenefeldia* Kunth, *Sesamum* L., *Shuteria* Wight et Arn., *Stephania* Lour., *Strombosia* Bl., *Telosma* Cov., *Tenagocharis* Hochst., *Thelepogon* Roth, *Tiliacora* Colebr., *Tinospora* Miers, *Vossia* Wall. et Griff. 101 (92)

2. Africa, Madagascar, etc., and Asia (often extending into Australasia and the Pacific Islands).

Achyrosperrum Bl., *Acridocarpus* Guill. et Perr., *Acrocephalus* Benth., *Adenia* Forsk., *Alangium* Lam. and *Marlea* Roxb., *Albizzia* Durazz., *Alloteropsis* Presl, *Alysicarpus* Neck., *Amorphophallus* Bl., *Anisophyllea* R. Br., *Apodytes* E. Mey., *Aponogeton* L. f., *Arduina* Mill. and *Carissa* L., *Artabotrys* R. Br., *Asteracantha* Nees *, *Asystasia* Bl., *Azima* Lam., *Baphia* Afzel., *Blyxa* Norr., *Borassus* L., *Bothriochloa* Kuntze, *Bridelia* Willd., *Bruguiera* Lam., *Canarium* L., *Canscora* Lam., *Casuarina* L., *Centipeda* Lour., *Ceriops* Arn., *Ceropegia* L., *Cheirostylis* Bl., *Cirrhopetalum* Lindl., *Cleistanthus* Hk. f., *Cnestis* Juss., *Coffea* L., *Commiphora* Jacq., *Corymbis* Thou., *Crossandra* Salisb., *Cryptolepis* R. Br. and *Ectadiopsis* Benth., *Deeringia* R. Br., *Dichrostachys* Wight et Arn., *Dicoma* Cass., *Disperis* Sw., *Dumasia* DC., *Ecbolium* Kurz, *Emilia* Cass., *Enhalus* L. C. Rich., *Enteropogon* Nees, *Ethulia* L. f., *Exacum* L., *Filicium* Thw., *Flagellaria* L., *Gaertnera* Lam., *Garcinia* L., *Gastonia* Comm., *Gelonium* Roxb., *Geniosporum* Wall., *Gerbera* Cass., *Giseckia* L., *Gloriosa* L., *Gnidia* L. and *Lasiosiphon* Fres., *Grangea* Adans., *Grewia* L., *Gymnema* R. Br., *Gynura* Cass., *Helinus* E. Mey., *Hemarthria* Munro, *Holmskioldia* Retz., *Hugonia* L., *Hydrilla* L. C. Rich., *Hydrophylax* L. f., *Hymenodictyon* Wall., *Hypoestes* Soland., *Iodes* Bl., *Iphigenia* Kunth, *Laggera* Sch.-Bip., *Laurembergia* Berg., *Lepironia* L. C. Rich., *Lumnitzera* Willd., *Macaranga* Thou., *Maesa* Forsk., *Medinilla* Gaudich., *Memycylon* L., *Mezoneuron* Desf., *Micrargeria* Benth., *Micrococca* Benth., *Microglossa* DC., *Moschosma*

Reichb., *Mundulea* Benth., *Mussaenda* L., *Myrsine* L., *Neyraudia* Hk. f., *Nothosaerva* Wight, *Oberonia* Lindl., *Ochna* L., *Odina* Roxb., *Olax* L., *Olea* L., *Orthosiphon* Benth., *Osbeckia* L., *Paropsia* Nor., *Pavetta* L., *Pedaliium* L., *Pemphis* Forst., *Peristrophe* Nees, *Phaius* Lour., *Phayloopsis* Smith., *Phoentx* L., *Pleurostylia* Wight et Arn., *Pollia* Thunb., *Polyalthia* Bl., *Premna* L., *Pseudarthria* Wight et Arn., *Rhamphicarpa* Benth., *Rhinacanthus* Nees, *Rungia* Nees, *Saccolabium* Bl. and *Acampe* Lindl., *Satyrium* Sw., *Scolopia* Schreb., *Sebaea* Soland.*, *Secamone* R. Br. and *Toxocarpus* Wight et Arn., *Smithia* Ait., *Sopubia* Buch-Ham., *Sphaeranthus* L., *Stereospermum* Cham., *Striga* Lour., *Strophanthus* DC., *Tarennia* Gaertn., *Thunbergia* Retz., *Toddalia* Juss., *Tricalysia* A. Rich., *Tristellateia* Thou. and *Hiptage* Gaertn., *Turraea* L., *Tylophora* R. Br., *Uraria* Desv., *Urophyllum* Wall., *Vangueria* Juss., *Ventilago* Gaertn., *Vepris* Comm., *Voacanga* Thou. and *Orchippeda* Bl., *Wiesneria* M. Mich., *Woodfordia* Salisb., *Xylia* Benth. 142 (142)

3. Madagascar, etc., and Asia (often extending into Australasia and the Pacific Islands).

Actinoschoenus Benth., *Agrostophyllum* Bl., *Agyneja* L., *Anacolosia* Bl., *Apluda* L., *Atylosia* Wight et Arn., *Balanophora* Forst., *Barringtonia* Forst.*, *Bleekrodea* Bl., *Byrsophyllum* Hk. f., *Carallia* Roxb., *Cephalostachyum* Munro, *Cerbera* L., *Cipadessa* Bl., *Cymbidium* Sw., *Ellertonia* Wight, *Erythrospermum* Lam., *Euodia* Forst. and *Melicope* Forst., *Geniostoma* Forst., *Givotia* W. Griff., *Hedychium* Koenig, *Melastoma* L., *Nepenthes* L., *Ochrocarpos* Thou., *Paederia* L., *Pongamia* Vent., *Pothos* L., *Samadera* Gaertn., *Sandoricum* Cav., *Schizostachyum* Nees, *Soulamea* Lam., *Strobilanthes* Bl., *Thuarea* Pers., *Tropidia* L., *Vateria* L., *Wormia* Rottb., *Zoisia* Willd. 37 (32)

4. Africa and/or Madagascar, etc., and Australasia.

Adansonia L., *Athrixia* Ker-Gawl., *Caesia* R. Br., *Cunonia* L., *Hibbertia* Andr., *Keraudrenia* J. Gay, *Rulingia* R. Br., *Triraphis* R. Br. 8 (8)

c. America and Asia (often extending into Australasia and the Pacific Islands).

Anaxagorea St. Hil., *Bocagea* St. Hil., *Callicarpa* L., *Capsicum* L., *Engelhardtia* Leschen. and *Oreomunnea* Oerst., *Enydra* Lour., *Gilibertia* R. et P., *Helicteres* L., *Ichnanthus* Beauv., *Inocarpus* Forst., *Klugia* Schlecht., *Laplacea* H. B. et K., *Lespedeza* Michx., *Linostoma* Wall. and *Lophostoma* Meissn., *Mappia* Jacq., *Meliosma* Bl., *Microtropis* Wall., *Mitreola* R. Br., *Oxybaphus* L'Hérit., *Physurus* L. C. Rich., *Roucheria* Planch., *Sageretia* Brongn., *Sapindus* L.*, *Saurauja* Willd., *Schoepfia* Schreb., *Sloanea* L. and *Echinocarpus* Bl., *Spathiphyllum* Schott, *Symplocos* Jacq., *Talauma* Juss., *Thismia* W. Griff., *Turpinia* Vent., *Xylosma* Forst. f. 32 (32)

d. America and Australasia only.

Distichlis Raf., *Lindenia* Benth., *Nicotiana* L., *Orthosanthos* Sweet, *Trichocline* Cass.* 5 (5)

e. Discontinuous over a considerable part of the Tropical Zone.

Arundinaria Michx., *Byttneria* Loebl., *Calliandra* Benth., *Camposperma* Thw., *Carapa* Aubl. and *Xylocarpus* Koenig, *Clethra* L., *Cochlospermum* Kunth, *Diplanthera* Thou., *Halophila* Thou., *Hermannia* L., *Hernandia* L., *Kalanchoe* Adams., *Lochnera* Reichb., *Lonchocarpus* H. B. et K., *Mimulus* L., *Omphalea* L., *Passiflora* L., *Protium* Burm. f., *Rhizophora* L., *Schrebera* Roxb., *Stephanotis* Thou. and *Jasminanthes* Bl., *Styrax* L., *Suriana* L., *Syringodium* Kütz., *Ternstroemia* Mutis., *Thalassia* Banks, *Turnera* L., *Weinmannia* L. 28 (20)

f. Anomalous genera of the Tropical Zone.

Aldrovanda Monti, *Brasenia* Schreb., *Buxus* L., *Canarina* L., *Cohnia* Kunth, *Cossinia* Comm., *Cytinus* L., *Fagonia* L., *Hydrodea* N. E. Br., *Kissenia* R. Br.,

Nesogenes A. DC., *Pelargonium* L'Hérit., *Pharnaceum* L. and *Hypertelis* E. Mey., *Phyllica* L., *Pilostyles* Guill., *Ruthea* Bolle 16 (10)

C. Genera found entirely or predominantly in the South Temperate Zone.

a. America and Australasia. 33 (32)

1. America, Australia and New Zealand, sometimes reaching the Pacific Islands.
Abrotanella Cass., *Aristotelia* L'Hérit., *Carpha* Banks et Soland., *Colobanthus* Bartl., *Discaria* Hook., *Donatia* Forst., *Drapetes* Banks, *Hebe* Comm., *Libertia* Spreng., *Lilaopsis* Greene, *Muehlenbeckia* Meissn., *Nothofagus* Bl., *Oreomyrrhis* Endl., *Pernetia* Gaudich. and *Gaultheria* L., *Schizeilema* Domin, *Selliera* Cav., *Uncinia* Pers. 17

2. America and Australia, sometimes reaching the Pacific Islands.
Drimys Forst., *Embothrium* Forst., *Eucryphia* Cav., *Lomatia* R. Br. 4

3. America and New Zealand.
Azorella Lam.*, *Enargea* Banks, *Fuchsia* L., *Gaimardia* Gaudich., *Griselinia* Forst., *Jovellana* R. et P., *Laurelia* Juss., *Marsippospermum* Desv., *Ourisia* Comm., *Phyllachne* Forst., *Pseudopanax* C. Koch, *Rostkovia* Desv. 12

b. Africa and Australasia only.
Anacampteros L., *Arctotis* L. and *Cymbonotus* Cass., *Australina* Gaudich., *Bulbine* L., *Bulbinella* Kunth, *Chrysitrix* L., *Dietes* Salisb., *Helipterum* DC., *Hypolaena* R. Br., *Restio* L., *Villarsia* Vent., *Wurmbea* Thunb. 12 (12)

c. Anomalous genera.
Carpobrotus N. E. Br., *Chevreulia* Cass., *Leptocarpus* R. Br., *Pringlea* Anders., *Tetragonia* L. 5 (5)

D. Genera found in both North and South Temperate Zones.

a. North Temperate Zone, and S. America, S. Africa and Australasia.
Erodium L'Hérit., *Frankenia* L., *Geum* L., *Koeleria* Pers., *Myosotis* L., *Myosurus* L., *Thesium* L., *Triglochin* L., *Viola* L., *Zostera* L. 10 (9)

b. North Temperate Zone, S. America and Australasia.
Calandrinia H., B. et K., *Caltha* L., *Coriaria* L., *Daucus* L., *Euphrasia* L., *Gentiana* L., *Glycyrrhiza* L., *Montia* L., *Myrtus* L., *Scleranthus* L. 10 (10)

c. North Temperate Zone, S. Africa and Australasia.
Emex Neck., *Kochia* Roth., *Limonium* Mill., *Papaver* L., *Trigonella* L., *Zygophyllum* L. 6 (7)

d. North Temperate Zone and S. Africa.
Althenia Petit*, *Cryophytum* N. E. Br., *Herniaria* L., *Oligomeris* Cambess., *Pityranthos* Viv., *Seetzenia* R. Br., *Sium* L.* 7 (5)

e. North Temperate Zone and Australasia.
Angelica L., *Damasonium* Mill., *Nitraria* L., *Posidonia* Koenig, *Saussurea* DC., *Sparganium* L., *Veronica* L.* 7 (9)

f. North Temperate Zone and S. America.
Adenocaulon Hk. f., *Antennaria* Gaertn., *Armeria* Willd., *Chrysosplenium* L., *Cicendia* Adans., *Drusa* DC.*, *Empetrum* L., *Honkenya* Ehrh., *Hymenolobus* Nutt., *Lardizabala* R. et P. and *Parvatia* Decne., *Lepuropetalon* Elliott, *Littorella* Berg., *Phippsia* R. Br., *Primula* L., *Saxifraga* L., *Sibthorpia* L. 16 (13)

E. Genera of various distribution but all with outlying species in the Hawaiian Islands.

a. Entirely or predominantly Old World.
Alectryon Gaertn., *Alphitonia* Reissek., *Alyxia* Banks, *Antidesma* L., *Byronia* Endl., *Canthium* Lam., *Claoxylon* A. Juss., *Coprosma* Forst., *Cordyline* Comm.,

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